Burmese pythons in Florida:
A synthesis of biology, impacts, and management tools

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Abstract

Burmese pythons (*Python molurus bivittatus*) are native to southeastern Asia, however, there is an established invasive population inhabiting much of southern Florida throughout the Greater Everglades Ecosystem. Pythons have severely impacted native species and ecosystems in Florida and represent one of the most intractable invasive-species management issues across the globe. The difficulty stems from a unique combination of inaccessible habitat and the cryptic and resilient nature of pythons that thrive in the subtropical environment of southern Florida, rendering them extremely challenging to detect. Here we provide a comprehensive review and synthesis of the science relevant to managing invasive Burmese pythons. We describe existing control tools and review challenges to productive research, identifying key knowledge gaps that would improve future research and decision making for python control.

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Introduction

Burmese pythons (*Python molurus bivittatus*, see Taxonomy section) are oviparous (egg-laying), nonvenomous, large, constricting snakes native to southeastern Asia (Bhupathy 1995; Barker and Barker 2008). However, they now inhabit the Greater Everglades Ecosystem which encompasses much of southern Florida. These snakes are dietary generalists with large home ranges and broad habitat requirements. They feed on a wide array of mammals, birds, and reptiles, and their introduction has had severe impacts on native species and ecosystems in the region. Successful python control involves an understanding of their basic biology (e.g., survival, reproduction) to inform population-size estimates that can be used to evaluate control tools to inform management and monitoring decisions.

The Greater Everglades Ecosystem consists of a vast, shallow, watershed 87 km (60 miles) long and 161 km (100 miles) wide (Lodge 2010). It is composed of a network of parks and preserves including Everglades National Park (ENP), Big Cypress National Preserve (BICY), Collier-Seminole State Park (CSSP), Fakahatchee Strand Preserve State Park (FSPSP), Picayune Strand State Forest (PSSF), Rookery Bay National Estuarine Research Reserve (RBNERR), Biscayne National Park (BISC), and Arthur R. Marshall Loxahatchee National Wildlife Refuge (LNWR; Table 1, Fig. 1), as well as numerous public and private conservation lands and property managed by the South Florida Water Management District and the Florida Fish and Wildlife Conservation Commission. These properties cover thousands of square kilometers of mostly uninhabited and not easily accessible land representing the largest natural subtropical wetland of its kind in the eastern United States.

Although Burmese pythons were found in the Greater Everglades as early as 1979 (Snow et al. 2007a), they were considered individual escapes or releases until the late 1990s and early 2000s when confirmation of a reproducing population in ENP prompted their recognition as an established invasive species (Meshaka et al. 2000). In the four decades since the first individual was recorded, the python population has

Table 1. Locations or entities referenced in this manuscript and the corresponding acronym.

Location, Agency, or Term	Acronym
Arthur R. Marshall Loxahatchee National Wildlife Refuge	LNWR
Big Cypress National Preserve	BICY
Biscayne National Park	BISC
Close-kin mark-recapture	CKMR
Collier-Seminole State Park	CSSP
Convention on International Trade in Endangered Species of Wild Fauna and Flora	CITES
Conservancy of Southwest Florida	CSWFL
Crocodile Lake National Wildlife Refuge	CLNWR
Department of Interior	DOI
Everglades and Francis S. Taylor Wildlife Management Area	Everglades WMA
Everglades National Park	ENP
Fakahatchee Strand Preserve State Park	FSPSP
Florida Department of Environmental Protection	DEP
Florida Fish and Wildlife Conservation Commission	FWC
Frog Pond Wildlife Management Area	Frog Pond WMA
Hole-in-the-Donut Restoration Area	Hole-in-the-Donut
International Commission on Zoological Nomenclature	ICZN
National Park Service	NPS
Pa-hay-okee Road	Pa-hay-okee
Picayune Strand State Forest	PSSF
Rookery Bay National Estuarine Research Reserve	RBNERR
South Florida Water Management District	SFWMD
Stormwater Treatment Area	STA
United States Fish and Wildlife Service	USFWS
United States Geological Survey	USGS
United States Department of Agriculture	USDA
Water Conservation Area	WCA
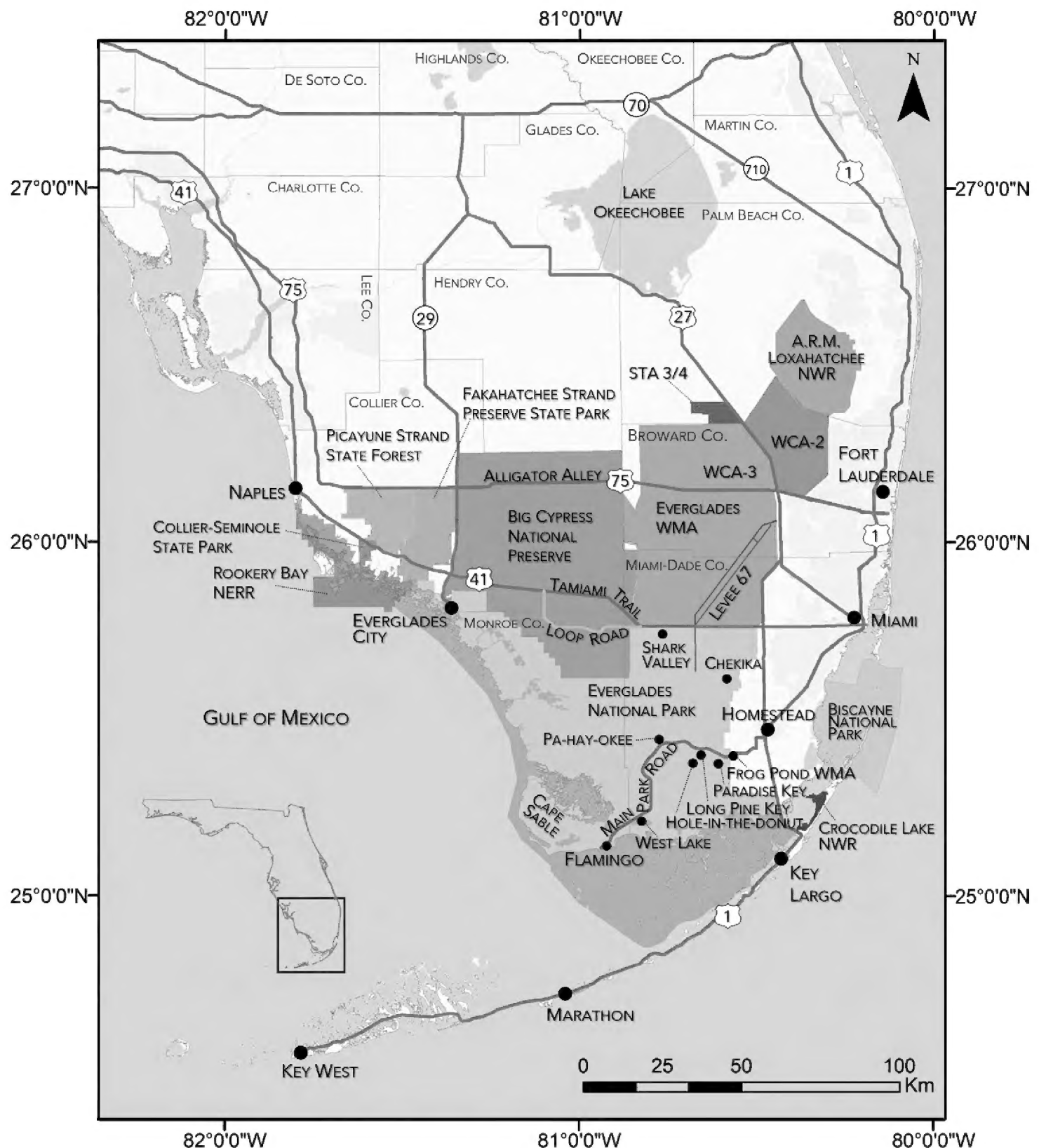
Figure 1. General Burmese python (*Python molurus bivittatus*) research areas across southern Florida (inset, black box). Primary research areas are indicated by green shaded polygons or black dots. Large black dots indicate major cities and gray lines indicate major roads; the beige line indicates Loop Road (unpaved). Levee-67 continues into ENP (L-67X). Abbreviations include Arthur R. Marshall Loxahatchee National Wildlife Refuge (LNWR), Everglades and Francis S. Taylor Wildlife Management Area (Everglades WMA), Water Conservation Areas (WCA 2 and 3), Stormwater Treatment Area 3/4 (STA 3/4), Pa-hay-okee Road (Pa-hay-okee), Hole-in-the-Donut Restoration Area (Hole-in-the-Donut), Frog Pond Wildlife Management Area (Frog Pond WMA), Rookery Bay National Estuarine Research Reserve (RB-NERR), and Crocodile Lake National Wildlife Refuge (CLNWR). Faint gray lines are county boundaries.

grown and spread, consuming native wildlife and altering the food web in the Everglades (Dorcas et al. 2012; McCleery et al. 2015; Willson 2017). A concerted effort by scientists to understand their biology and explore control tools began in earnest in late

2005, and numerous research projects have made strides toward this goal. Shortly after, Reed and Rodda (2009) reviewed the biology and management of nine species of giant constrictors including Burmese pythons. Since then, much has been learned about invasive Burmese pythons, and this comprehensive synthesis of python biology and control tools is intended to: (1) review and synthesize the body of science relevant to managing invasive Burmese pythons, (2) interpret the results of our synthesis to provide managers information about control options, and (3) highlight key scientific uncertainties to guide future research.

In this synthesis we discuss Burmese python biology as it relates to management of the species, including insights from research on their taxonomy, demography, and physiology. Second, we outline our current understanding of how Burmese pythons arrived in Florida. Third, we review one of the greatest challenges in managing Burmese pythons, low detectability, and progress addressing this challenge. We then discuss ecological and socioeconomic impacts of pythons and describe the distribution and movement ecology of the species. Finally, we describe existing control tools and review challenges to productive research, identifying key knowledge gaps that could improve future research and decision making for python control.

The authorship of this publication is diverse, representing many of the experienced scientists and managers involved with the Burmese python invasion over the last two decades, including representatives from United States federal agencies, the state of Florida, and numerous non-profit and academic institutions. This document represents the consensus of this scientific community, and in the few cases where consensus is not clear, multiple viewpoints are explored for better insight to drive future research.

Natural history of Burmese pythons

Identification

Burmese pythons have a distinct dorsal pattern of black-bordered, brown dorsal and lateral blotches separated by tan coloration that extends underneath to the venter (Fig. 2; Krysko et al. 2019a). The top of the head has a dark, triangular, spearhead-shaped region with a white line extending posteriorly under the eye. The venter is white, unpatterned, and bordered by black spots. Burmese pythons also have a sub-ocular scale just below the eye, differentiating them from *P. molurus molurus* (Fig. 2, see Taxonomy section), which has a 6th supralabial scale abutting the eye (O'Shea 2007).

Taxonomy

The status of the Burmese python as either a full species (*Python bivittatus* Kuhl, 1820) or a subspecies (*Python molurus bivittatus* Kuhl, 1820) of the Indian python (*Python molurus* Linnaeus, 1758) has been in flux for most of the past two centuries, and the taxonomy remains unstable today (McDiarmid et al. 1999; Reed and Rodda 2009).

The Burmese python was initially named and described using iconotypes (i.e., illustrations that serve as the type for the species description), which were later demonstrated to be the *Python sebae* species (Bauer and Günther 2013). Thus, the Burmese python has no type, and if elevated to species rank, a petition to the International Commission on Zoological Nomenclature (ICZN) is required to stabilize the name of *P. bivittatus* (Bauer and Günther 2013).

In general, there are geographic, morphological, and genetic characteristics suggesting that Indian and Burmese pythons may be distinct evolutionary lineages (i.e., they may fit the general lineage concept of species; de Queiroz 1999), but additional data would be useful. For example, Jacobs et al. (2009) suggested elevating the Burmese python to full species rank because Indian and Burmese pythons have been reported as syntopic in parts of their range (O'Shea 2007; Barker and Barker 2008), but they did not present new evidence for the taxonomic change, and Schleip and O'Shea (2010) later disputed the syntopy claim. Similarly, the presence or absence of a subocular scale has been used to distinguish Indian from Burmese pythons (O'Shea 2007), but because that scalation is not heritable in other python species (Branch and Erasmus 1984), it may be a poor character for species delimitation. Further, although Burmese and Indian pythons were recently identified as reciprocally monophyletic by Reynolds et al. (2014), the DNA-sequence data used in that analysis were obtained from the online repository GenBank, with unsuitable sample groupings for species delimitation (i.e., single terminals for each taxon) from a non-curated database (Reynolds et al. 2014). More specifically, because the two taxa were thought to be one species for many years, users may have categorized a Burmese python as *P. molurus*, which is now identified as the Indian python (see discussion in Hunter et al. 2018).

Taxonomic resolution for native-range Burmese pythons is of interest to the invasive population in Florida because there is evidence of hybridization between *P. molurus bivittatus* and *P. molurus molurus* - most likely before the introduction in Florida. In a sample of 426 pythons collected from locations throughout southern Florida between 2001–2012, two of six observed mitochondrial haplotypes were associated with 11 sequences from Indian pythons (Hunter et al. 2018). However, nuclear genetic evidence of recent hybridization was not found, resulting in cytonuclear discordance between the mitochondrial and nuclear genomes, most likely supporting past hybridization. Additional data from the native range are needed to rule out the less likely influence of natural selection. Thus far, the observed morphology of pythons collected in Florida is consistent with Burmese pythons (Hunter et al. 2018).

The geographic origin of ancestors to the Florida population is thought to be Thailand and Vietnam, based on the declared origin of most imports during the time when pythons were presumably introduced (Hoover 1998). Mixing of these two distinct lineages (i.e., Thailand/Vietnam and the Indian subcontinent) in the pet trade or in the wild may provide the Florida population with novel genomes to facilitate adaptation to a wider range of conditions (e.g., Hahn and Rieseberg 2017). Given the evidence of Indian python mitochondrial genomes in the Florida population (although limited in number), analyses that rely on aspects of taxonomy (e.g., species physiology, behavior) could benefit from considering both Burmese and Indian pythons.
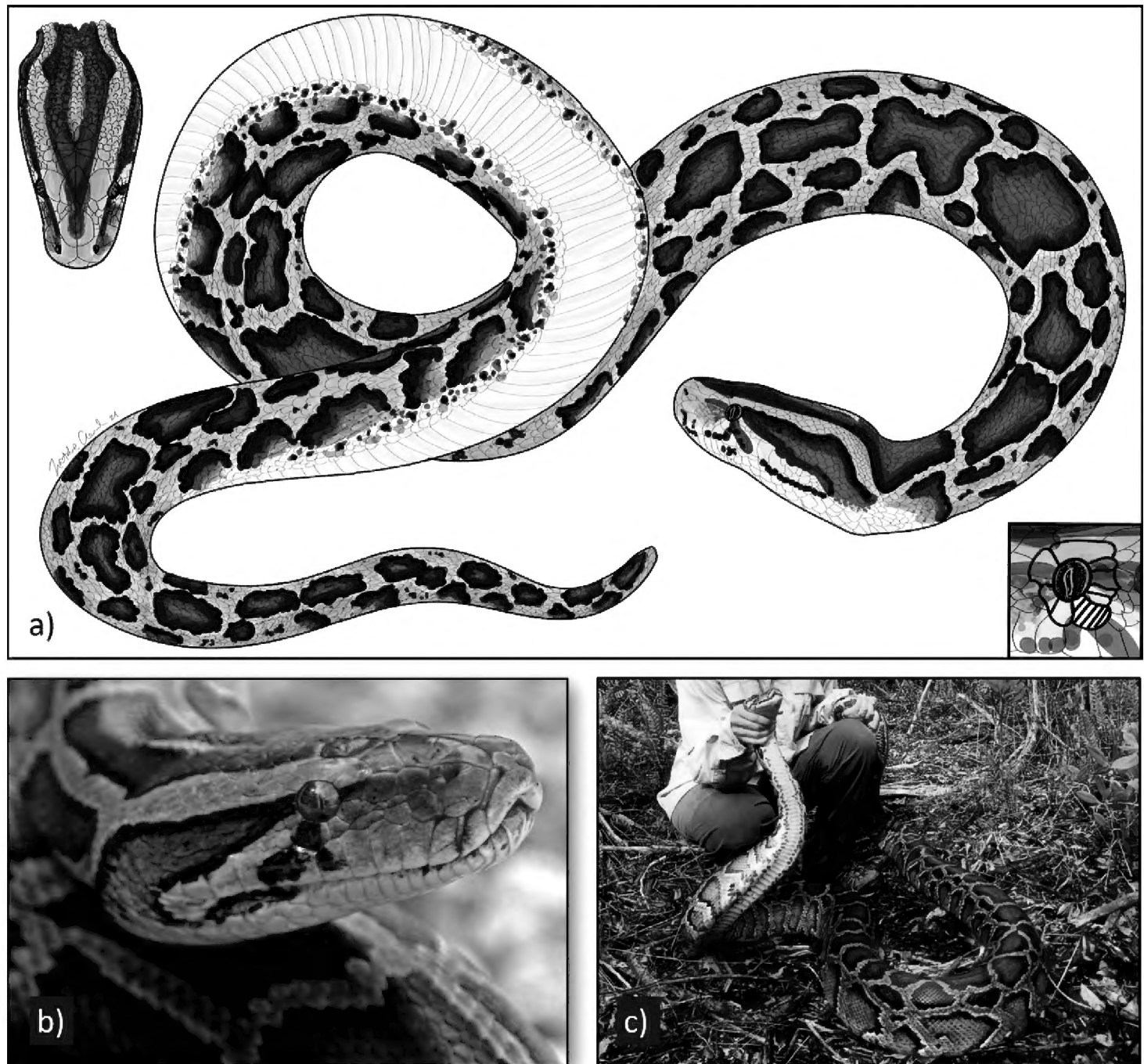
Figure 2. Identification of Burmese pythons (*Python molurus bivittatus*). Distinguishing features include **a, b** a dark triangular spearhead on the top of the head extending to snout, with a white line extending posteriorly under the eye **a** subocular scale just below the eye preventing contact between supralabial scales and the eye (hatched lines, inset), and **a, c** a pattern of black-bordered, brown dorsal and lateral blotches separated by tan coloration and a white, non-patterned venter bordered by black spots. Panel **a** illustrated by Natalie Claunch. Photo credits: U.S. Geological Survey (**b**) and Conservancy of Southwest Florida (**c**).

Ultimately, the large geographic range of Indian and Burmese pythons presents opportunities for isolation leading to speciation and undocumented cryptic diversity. Portions of the range are also thought to overlap, potentially allowing for historical mixing in those areas. Thus, more genetic information from the native range would be needed to resolve this issue (Hunter et al. 2018). Understanding the taxonomy is important to understand adaptation potential, parameterize climate models, and interpret genetic data. Although python morphology in Florida is consistent with the species-level distinction (*P. bivittatus*, Hunter et al. 2018), in this document, we recognize the hybridization and taxonomic instability discussed above, and therefore, use the name *P. molurus bivittatus* for Burmese pythons in Florida.

Demography

Central to Burmese python management is understanding demography, or how vital rates (such as survival, growth, and reproduction) structure python populations. Changes in these birth and death processes drive changes in abundance over time and space (i.e., population ecology). Key demographic information can be summarized in a life table, which is a record of survival and reproductive rates in a population, broken down by age, size, or developmental stage (e.g., egg, hatchling, young of year, juvenile, sub-adult, adult). Information from life tables can be used to build a structured population model that can predict how changes to life-history parameters influence growth or decline of populations over time and thus how control tools might affect population dynamics. There is currently little information to construct a life table for Burmese pythons. However, future research to estimate life table parameters and develop a structured population model can help identify aspects of Burmese python life history of relevance to management efforts. For example, pinpointing the demographic parameters (e.g., age, stage, or size class) that contribute most to population growth can inform targeted removal efforts. An understanding of Burmese python vital rates can also identify potential hurdles to management efforts. For example, control efforts for invasive American bullfrogs (*Lithobates catesbeianus*) that focus on removing tadpoles and breeding adults can be offset by density-dependent competition and reduced cannibalism, so are less effective at decreasing population growth rate compared to seasonal culling of metamorphs (Govindarajulu et al. 2005). This type of understanding can help managers target age, stage, or size classes that are most likely to create additive, rather than compensatory, mortality in the population (see Challenges Interpreting Removal Data).

Survival

Annual survival has not been well characterized for Burmese pythons, in part because requisite sample sizes and study durations for telemetry-based estimations are logistically and financially challenging (Murray 2006). However, survivorship is presumably high because adult Burmese pythons in southern Florida reach sizes that are too large for most predators to kill them. Using survival estimates based on professional judgement and informed by rates calculated for large snake species such as the Australian water python, *Liasis fuscus* (Madsen et al. 2006), Willson et al. (2011) postulated a 90% annual survival rate for adult Burmese pythons under typical weather conditions in southern Florida.

As with adult pythons, there are few empirical data available to inform estimates of juvenile survival rates. Pittman and Bartoszek (2021) used radiotelemetry to monitor 28 hatchling Burmese pythons from 4 clutches in southwestern Florida. Radiotelemetry involves attaching a radiotransmitter to an animal, or, in the case of pythons, implanting a transmitter within the body cavity and using a receiver and directional antenna to locate telemetered individuals. Overall, 6-month survival was 35.7% (95%

CI = 18–53%), and annual survival was 28.6% (12–45%), with only 2 (7.1%) confirmed to have survived 2 years post release. Survival of neonate pythons to 6 months was lower for snakes from 'human-modified' habitats (~20% 6-mo survival; agricultural interface or urban areas) compared to natural habitats (~50% 6-mo survival; forested wetlands or upland pine areas), but after 12 months, there was no difference in survival (Pittman and Bartoszek 2021). However, because pythons at each release location were from separate clutches, differences in survival among habitats could be attributable to genetic or developmental differences between clutches (Pittman and Bartoszek 2021). For example, despite experimental manipulation of food availability for two clutches of Burmese pythons, phenotypic variation in neonate growth has been attributed to clutch effects rather than feeding treatment or sex (Josimovich et al. 2021).

There are few published data on clutch or egg survival of wild Burmese pythons. However, brooding females are capable of shivering thermogenesis to raise embryonic temperatures during cool periods and exhibit parental care via nest attendance, which together likely increase embryo survival by discouraging potential nest predators (e.g., Currylow et al. 2022a) and maintaining optimal temperatures for development (see Reproduction section). Female pythons may also nest in refugia such as armadillo and tortoise burrows, within thick vegetation, or in manmade structures (see Habitat Use section) which may also help reduce nest predation and maintain optimal temperatures. Of the published accounts, two monitored python nests had hatch success rates of 77% and 92% (Hanslowe et al. 2016; Wolf et al. 2016; see Reproduction section).

Mortality

In their native range, king cobras (*Ophiophagus hannah*, Krishna 2002) and raptors (crested serpent eagle, *Spilornis cheela*; Goel et al. 2017) are documented predators, and pythons have been trampled by ungulates or killed during or after consuming difficult prey (e.g., porcupine and horned ungulates; Wall 1921; Bhupathy and Vijayan 1989). Other possible predators include tigers (Wall 1921), jackals, and hyena. Additionally, monitor lizards may prey on eggs (Bhupathy and Vijayan 1989). In Florida, documented predators of Burmese pythons include bobcats (*Lynx rufus*; McCollister et al. 2021), indigo snakes (*Drymarchon couperi*; Andreadis et al. 2018), Florida cottonmouths (*Agkistrodon conanti*; Bartoszek et al. 2021a, Currylow et al. in press), black racers (*Coluber constrictor*; I. Bartoszek, CSWFL, Written Communication, 5/27/2021), American crocodiles (*Crocodylus acutus*; Godfrey et al. 2021), and American alligators (*Alligator mississippiensis*; Snow et al. 2006; Mazzotti et al. 2011; Smith et al. 2016; Currylow et al. in press). Additionally, a Florida black bear (*Ursus americanus floridanus*) caused a non-lethal injury to an adult female python (McCollister et al. 2021). Few native species are large enough to prey upon adult pythons, and thus far, alligators appear to be the primary predator of Burmese pythons. For example, at least six predation events of adult pythons by alligators and eight of hatchlings have been recorded in the literature (Snow et al. 2006; Mazzotti et al. 2011; Smith et al.

2016; Pittman and Bartoszek 2021; Currylow et al. in press), with additional reports in the media. It is not always clear whether predation by alligators is the result of direct predation or opportunistic scavenging of dead pythons, and the overall impact of alligator predation on python populations is unknown. Burmese python eggs are also vulnerable to predators such as bobcats (Currylow et al. 2022a), and in laboratory experiments have been preyed upon by the invasive red imported fire ant (*Solenopsis invicta*, Diffie et al. 2010).

Undocumented but potential predators of Burmese pythons in southern Florida include Florida panthers (*Puma concolor coryi*), coyotes (*Canis latrans*), foxes (*Urocyon cinereoargenteus*, *Vulpes vulpes*), various avian species, and invasive species like the Nile monitor (*Varanus niloticus*, Mazzotti et al. 2020). Similarly, other invasive species, including spiny-tailed iguanas (*Ctenosaura* spp.) and Argentine black and white tegus (*Salvator merianae*), have been observed to agonistically kill medium-sized snakes in non-predatory attacks (Engeman et al. 2009; Kaiser et al. 2013) and may kill young Burmese pythons. Further, tegus are known nest predators (e.g., Mazzotti et al. 2015) and may consume python eggs. Hatchling and, in some cases, juvenile pythons are likely prey to the same predators as native snakes. For example, a wide variety of birds prey on snakes, especially raptors (e.g., hawks, eagles, kites) and wading birds (e.g., egrets and herons; Guthrie 1932; Fitch 1963; Mushinsky and Miller 1993; Sparkman et al. 2013). Because many meso-mammals consume snakes, including opossums (*Didelphis virginiana*), mustelids, skunks, foxes, raccoon (*Procyon lotor*), and feral hogs (Baker et al. 1945; Jolley et al. 2010; Voss and Jansa 2012; Stobo-Wilson et al. 2021), small pythons are likely vulnerable to these taxa. Indeed, numerous bite marks on both transmitters and associated hatchling python carcasses (Currylow et al. in press) suggest meso-mammal predation events may occur frequently, although scavenging likely also occurs. Not all documented python mortalities can be attributed to predation, and there is some evidence that Florida's ecosystem and environment could be playing a role. For example, Burmese pythons generally cannot survive exposure to sustained body temperatures below 5–10 °C (Avery et al. 2010; Dorcas et al. 2011; Mazzotti et al. 2011). An unusual cold spell during 2010 killed many wild pythons in southern Florida when air temperatures remained at or below 10 °C for at least 48 hours, culminating in lows of -4–0 °C on 11 January (Mazzotti et al. 2011; Smith et al. 2016). In the northern extent of their native range, Burmese pythons are thought to brumate during the winter in hibernacula (reviewed in Reed and Rodda 2009). In the subtropical region of southern Florida, some pythons apparently lack these behaviors, and instead, may attempt to bask during lethally cold periods instead of retreating to sheltered refugia (Avery et al. 2010; Dorcas et al. 2011; Mazzotti et al. 2011), resulting in mortality from exposure (see Potential Range and Physiology sections). Some mortality in juvenile pythons has been attributed to an inability to appropriately identify or handle prey items available in the Everglades. In one case, a large cotton rat (106% of the hatchling python's body weight), was thought to inflict mortal wounds prior to python predation (Currylow et al. in press).

Humans are thought to be the primary cause of mortality for Burmese pythons in their native range, largely due to habitat loss and over-collection (Groombridge and Luxmoore 1991). Within their introduced range, humans are sources of mortality because of deliberate removal (e.g., Mazzotti et al. 2016), vehicular mortality, and agricultural activities such as mowing and discing (Mazzotti et al. 2011; Reed et al. 2011). However, the Greater Everglades Ecosystem is vast and remote (see Introduction), and the interior is difficult to survey. Therefore, humans may be the principal source of adult python mortality only in areas where and when python removal is actively occurring. Outside of these areas, most wild python mortality is likely a result of predation, abiotic factors, and senescence, and thus far mortality from pathogens (e.g., nidovirus, see Parasites and Pathogens section) has not been observed.

Reproduction

Burmese pythons in Florida typically mate over approximately 100 days during winter and early spring (early December to mid-March), when males seek and aggregate around mature females (Smith et al. 2016; Currylow et al. 2022b) likely using chemical information to locate them (e.g., scent trailing; Mason and Parker 2010; Parker and Mason 2011, see Pheromone section). During this time, adult python gonadal resurgence is observed in both sexes and is generally correlated with body size and weight, peaking in females with developing follicles (Currylow et al. 2022b). Breeding aggregations of up to eight individual pythons have been documented in lowland forests (tree islands) that are slightly elevated above the surrounding wetland habitat in ENP (Smith et al. 2016), and mating season activity has been associated with elevated habitats such as xeric scrub and oak hammocks in southwestern Florida (Bartoszek et al. 2021b). Courtship of female Burmese pythons by males may be facilitated by the presence of external sexually dimorphic cloacal spurs which are remnants of the pelvic girdle and capable of movement. Presumably, these spurs, which are larger in males, are used to align male and female tails, possibly providing stimuli to the female to enhance receptivity (Gillingham and Chambers 1982). Overall, information on Burmese python courtship and mating is not well documented and much is based on anecdotal observations of long-term captive pythons (summarized in Richard et al. 2019; see Pheromone section).

In southern Florida, females can have primary follicles throughout the year, develop secondary follicles most frequently from December into March, then oviductal eggs from March into May, and lay eggs in May (Currylow et al. 2022b). Male Burmese pythons may have flaccid testes throughout the year, but many start to become semi-turgid in November in preparation for the breeding season, then become turgid December through March (Currylow et al. 2022b). Burmese python clutches appear to hatch synchronously approximately two months after oviposition in July (Currylow et al. 2022b, see also Hanslowe et al. 2016). This timeline is consistent with the appearance of hatchlings on the landscape in July and August as they disperse from nests (Falk et al. 2016; Currylow et al. 2022b). Estimates of incubation time for captive

animals range from 58–68 days (Wall 1921; Vinegar 1973; Van Mierop and Barnard 1976a; Wagner 1976; Clercq 1988), however, incubation time is presumably influenced by temperature and may vary considerably for wild pythons. The frequency of reproduction in the wild is not well established, largely because reproductive changes to ovaries and oviducts are short-lived and not always observable during necropsies (B. Falk, NPS, Written Communication, 12/22/2020), and longer-term monitoring of robust numbers of reproductive adult females has not occurred. However, Currylow et al. (2022b) found that 36% of females were non-reproductive in any given year and suggesting that some female pythons in Florida may only oviposit every 2–3 years. Though some radiotelemetered wild females have been observed to oviposit in consecutive years (I. Bartoszek, CSWFL, Written Communication, 5/27/2021), presumably as a result of abundant prey, most are thought to oviposit clutches biennially because time is needed to recover from the energetic demands of producing and brooding eggs (Reed and Rodda 2009). For example, one female Burmese python lost 54% of her body weight while breeding, laying, and incubating eggs (Wolf et al. 2016), although another was found to be 113% of of her pre-nesting weight the month after incubation ceased (Currylow et al. 2022a).

Despite their prevalence in captivity (Hoover 1998, see History of Imports section), Burmese pythons have only twice been documented reproducing without a male or stored sperm (i.e., parthenogenesis; Groot et al. 2003; Booth et al. 2014), a reproductive strategy thought to have evolved under conditions of low male-female encounter rates (Rivas and Burghardt 2005). It is not known how often parthenogenesis occurs in wild Burmese pythons. Multiple paternity (i.e., more than one male siring a clutch) has been documented in the Florida population (Skelton et al. 2021) and likely increases genotypic diversity (i.e., combinations of alleles). However, multiple paternity is not expected to increase allelic diversity (i.e., number of variants at each place in the genome) because this only increases through additional introductions or mutations which do not typically occur over ecological timescales.

In the low-elevation ecosystem of southern Florida, elevated habitats that remain relatively dry are important for nesting. In southwestern Florida where natural areas are interspersed with urban development, elevations of ~1.7 m have been associated with python nest site-selection, with nests concentrated on the urban fringe of the development, borders of agricultural fields, or in sandy upland habitat (Bartoszek et al. 2021b). In the more contiguous habitat of ENP, pythons likely use similarly elevated habitat for nesting to protect against seasonal flooding. However, anthropogenic structures such as dry culverts, canal banks, and debris piles are also used (Snow et al. 2007b; Hanslowe et al. 2016), likely because these areas tend to be elevated above standing water.

Clutch size of Burmese pythons increases with body size (Willson et al. 2014; Currylow et al. 2022b) and in Florida, has been reported to vary between 11 and 84 eggs, although very large snakes (~470–480 cm snout-vent length, SVL) have been reported to contain as many as 79–87 oviductal eggs (Table 2). However, reports of the number

of Burmese python eggs per female may be confounded by their gonad developmental stage and have been known to include vitellogenic follicles. This type of enumeration is typical for females removed and later necropsied, and likely results in an overestimate of true clutch size (see Currylow et al. 2022b). Data specific to oviductal eggs (i.e., those more likely to actually be laid) or wild nests are sparser but suggest an average clutch size of 34 in southern Florida (Currylow et al. 2022b; Table 2). Equations to estimate potential clutch size based on female body size have been developed (e.g., for oviductal eggs only = -35.8948 + 0.2306006*SVL (cm)), a tool that removal programs may benefit from when estimating efficacy (Currylow et al. 2022b; see Removal Programs section). After egg deposition, female pythons provide parental care by wrapping their bodies around the clutch (i.e., brooding eggs), apparently affording protection and preventing desiccation (Stahlschmidt and DeNardo 2010). Burmese pythons have been observed actively defending nests against predators (Currylow et al. 2022a) and females can modify the nest temperature through shivering thermogenesis, wherein females generate heat by repeatedly contracting their muscles (Hutchison et al. 1966; Snow et al. 2010). Laboratory studies have documented increased muscle contraction rate with decreasing nest temperatures, such that females are able to raise the temperature of the clutch by as much as 4 to 7 °C above ambient temperatures, depending on female body size (Hutchison et al. 1966). Likewise, a field study in ENP recorded a mean nest temperature of 29.2 °C (range = 26.9–33.6 °C), despite a mean ambient air temperature of 28.0 °C (range = 21.2–43.4 °C; Snow et al. 2010), and shivering thermogenesis may increase Burmese python embryo survival (see Survival section). Although an optimal developmental temperature of approximately 33 °C has been suggested in captivity (Brashears and DeNardo 2013), limited data on wild Burmese python nests in ENP during July reported mean temperatures of ~28–29 °C (Snow et al. 2010; Wolf et al. 2016). Burmese pythons possess XY sex chromosomes and sex determination is genetic (Gamble et al. 2017), generating roughly equal numbers of males and females. Thus far, two Burmese python nests in southern Florida have exhibited a slight male bias that may be related to small sample sizes (47% female, 53% male, n = 17 eggs, Wolf et al. 2016; 38% female, 62% male, n = 16 eggs, Hanslowe et al. 2016).

Given brooding and nest-temperature maintenance by females, clutch survival is presumably high, and this is supported by data from a handful clutches, with hatching-success rates of 92% (n = 25 eggs; Hanslowe et al. 2016), 77% (n = 22 eggs; Wolf et al. 2016), and 78%, 88% and 95% (n = 40, 79, and 39 eggs respectively; Currylow et al. 2022b). However, not all eggs in a clutch may be viable. Wild Burmese python nests have been documented with visibly smaller and/or discolored eggs relative to the rest of the clutch and these eggs did not hatch (i.e., 1/24 and 6/40 eggs were inviable; Currylow et al. 2022b). Further, several female Burmese pythons captured outside of the oviposition period in Florida contained eggs that were wrinkled or shrunken, and it is unknown why they failed to develop, if they are a result of maladaptation to the non-native ecosystem, or if egg retention influences python fitness or population dynamics (Anderson et al. 2022).

Table 2. Current estimates of Burmese python (*Python molurus bivittatus*) demographic parameters by life stage in southern Florida, USA. Dash indicates data for parameter does not exist. Four example developmental stage classes are included. Asterisk (*) indicates Rookery Bay Estuarine Research Preserve and Collier-Seminole State Park. Reported clutch size values (^^) can include large pre-ovulatory follicles, oviductal eggs, or laid eggs, whereas data specific to oviductal eggs (i.e., those more likely to actually be laid) are indicated by a plus symbol (+) in the Notes column. Caret symbol (^) indicates data are based on individuals that have secondary follicles (i.e., pre-ovulatory, late-vitellogenic follicles).

Annual survival						
Age/Size Class	Estimate	95% CI	Sample size	Location	Reference	Notes
Hatchling	29%	12–45%	28	southwest Florida*	Pittman and Bartoszek 2021	6-mo survival: 35.7% (21–60%); 2 of 28 survived 2yr post-release
Juvenile	–	–	–	–	–	–
Subadult	–	–	–	–	–	–
Adult	–	–	–	–	–	–

Fecundity						
Reproductive frequency	Annual	Biannual				
	–	–	36% (n = 67 of 184) of adult ♀'s non-reproductive annually (Currylow et al. 2022b)			
	Python length		Clutch size^^	Sample Size		
	SVL (cm)	TL (cm)	mean (range)	(# of clutches)		
Clutch size	264-286	297-322	(21-37)	7	Krysko et al. 2008, Snow et al. 2010, Hanslowe et al. 2016, Wolf et al. 2016	
	184-292	210-328	22 (2-56)	75	Currylow et al. 2022c	+ mean: 21 (2-41)
	295-376	332-427	45 (27-74)	27		+ mean: 39 (27-59)
	377-401	431-455	64 (42-86)	11		+ mean: 60 (52-64)
	408-478	460-533	75 (35-103)	16		+ mean: 53 (35-72)
	424-482	430-537	(61-87)	7	Krysko et al. 2008, 2012; Rochford et al. 2010a, Josimovich et al. 2021	
	Number hatched	% Hatched				
Hatching rate	17 of 22	77			Wolf et al. 2016	
	50 of 61	82			Josimovich et al. 2021	
	71 of 71	100			Josimovich et al. 2021	

Minimum Female Size at Maturity				
	Python length		Sample size	
Minimum size at maturity	SVL (cm)	TL (cm)		
	185	210	2	Willson et al. 2014, Currylow et al. 2022b
Average minimum Size at maturity^	206♀, 182♂		80♀, 246♂	Currylow et al. 2022b
Age at maturity	–	–		
Longevity	–	–		

Size distribution

Burmese pythons exhibit female-biased sexual size dimorphism with females larger than males, both in length, by as much as 150–180 cm, and mass, with the heaviest

of females nearly twice as heavy as the largest males (85 kg vs 44 kg; Reed and Rodda 2009; Falk et al. 2017; Currylow et al. 2022b). This dimorphism is consistent with significant maternal investment by reproducing females, which undergo periods of fasting facilitated by first building, and then depleting, large fat stores (see Reproduction section; Falk et al. 2017).

Burmese pythons in southern Florida vary in size from 34.44 to 500.9 cm SVL and 0.04–97.5 kg (n = 7,762; Figs 3, 4; Currylow et al. 2022b, c; Suppl. material 1). The distribution of observed python size is bimodal, with many observations of young pythons, including hatchling and young of year age classes less than 80 cm SVL, which comprise approximately 35% of observations (n = 2,698; Fig. 3, see Hatchling Size section). Adult pythons 160–240 cm SVL comprise 46% of observations (n=3,581; Fig. 3; see Size at Maturity section). Literature reports of Burmese python lengths are inconsistent in the units used to report body size, and often report SVL or TL, but not always both units. SVL is the standard unit used because it minimizes variation in total length attributed to potential tail damage. However, based on a large dataset of python morphologies, equations have been developed to define the expected relationships of SVL to TL (Currylow et al. 2022b):

1. Reproductive adult females:
   a. SVL (cm) = -4.25341 + 0.8954965*Total Length (cm)
   b. Total Length (cm) = 4.4790281 + 1.1165112*SVL (cm)
2. Reproductive adult males:
   a. SVL (cm) = -3.287218 + 0.8818756*Total Length (cm)
   b. Total Length (cm) = 4.5850061 + 1.1287574*SVL (cm)

Python length-mass relationships are influenced by sex, where females are typically heavier per unit length than males, as well as length, where longer snakes are proportionally heavier per-unit length than shorter snakes (i.e., allometric growth; Falk et al. 2017). Other factors influencing length-mass relationships could include spatiotemporal effects such as habitat type and prey availability and composition (e.g., Madsen and Shine 1993). Additionally, reproductive and digestive stages cause length-mass relationships to vary temporally (e.g., Currylow et al. 2022b). Finally, observed differences in mass-length relationships may be influenced by capture type, as programs that predominantly use scout snakes may find longer reproductive adult pythons (e.g., Smith et al. 2016) on-average, compared to pythons found during road cruising (Fig. 4; see Removal Program and Scout Snake sections), and these scout snake captures may be more heavy-bodied as well.

Hatchling size

Burmese pythons are large snakes, even as hatchlings. In their native range, hatchling mass varies from 75–165 g and TL varies from 48–79 cm long (SVL ~43–71 cm; Reed and Rodda 2009). Hatchling Burmese pythons are observed in southern Florida between July and October, peaking in August (Falk et al. 2016; Currylow et al. 2022b).
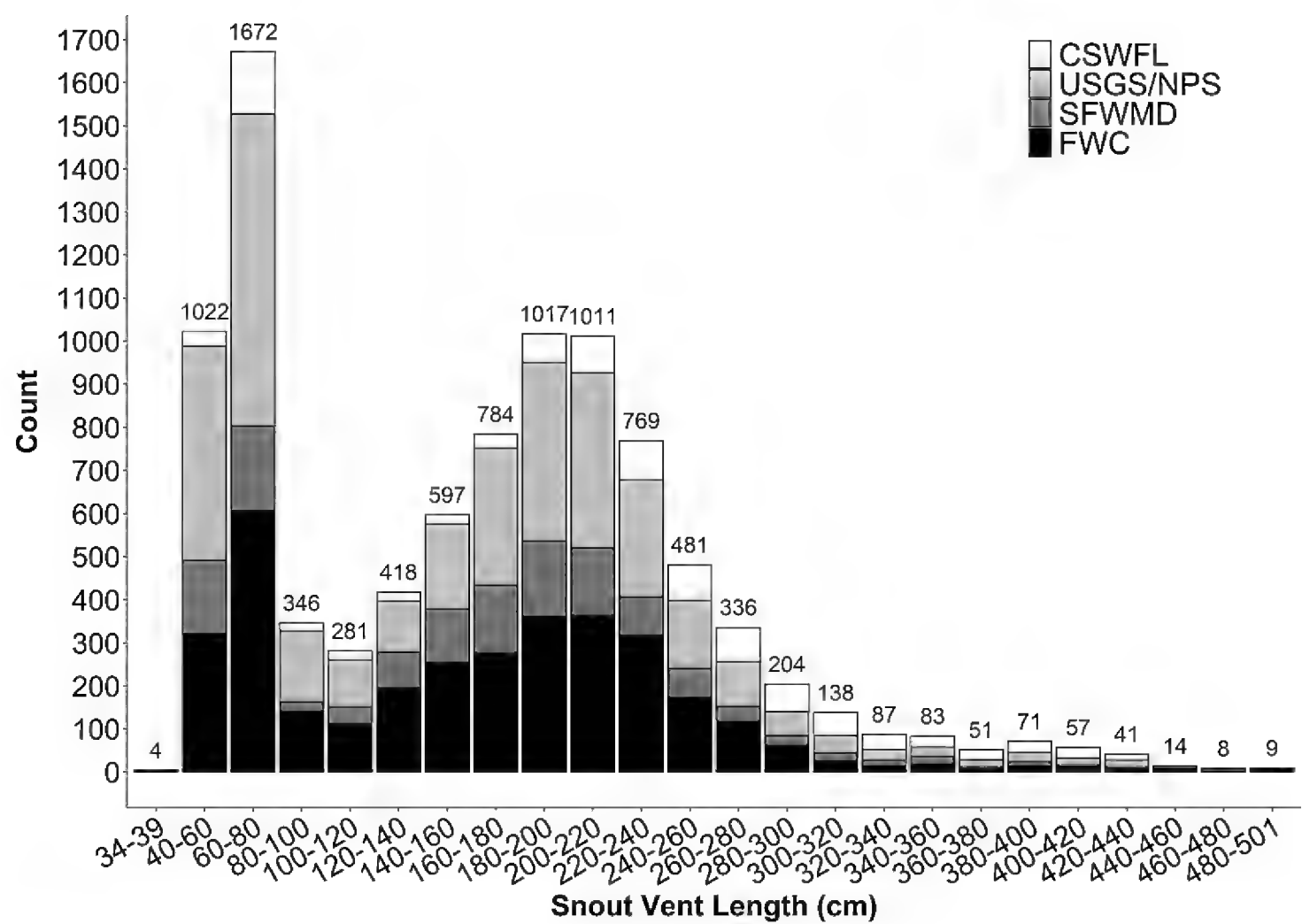
Figure 3. Distribution of Burmese python (*Python molurus bivittatus*) body size in southern Florida, USA (n = 9,501) varying from 34.44 cm to 500.9 cm SVL (snout-vent length). Bars represent pythons measured between 1995-2022 by state and federal agencies summarized by SVL. Data are from the U.S. Geological Survey and National Park Service (USGS/NPS, n = 3,723, Currylow et al. 2022c), Florida Fish and Wildlife Conservation Commission (FWC, n = 3,418, Suppl. material 1), South Florida Water Management District (SFWMD, n = 1,407, Suppl. material 1), and Conservancy of Southwest Florida (CSWFL, n = 959).

Data from eight clutches (120 neonatal hatchlings) indicate that SVL varies from 39–67 cm (Hart et al. 2012; Wolf et al. 2016; Josimovich and Currylow 2021), and young of year hatchlings average 63 cm SVL (Currylow et al. 2022b). These lengths correspond to total lengths of 44–75 cm based on estimates that tail length is approximately 12.6% of total length for juvenile pythons (Currylow et al. 2022b). Hatchling mass varies from 49 to 176 g (Hart et al. 2012; Wolf et al. 2016; Josimovich and Currylow 2021), averaging 125 g in the wild (Currylow et al. 2022b). A larger dataset of young of year pythons from Florida (n = 1,486) indicates that by November, juvenile pythons averaged 94 cm SVL (84–101 cm) at 548 g (360–680 g) and become indistinguishable from older juveniles from the previous year (Currylow et al. 2022b).

Florida has 51 native snake species and Burmese python hatchlings are generally larger than neonates of the five largest native species (eastern diamond backed rattlesnake, *Crotalus adamanteus*: 30–38 cm SVL; ratsnake, *Pantherophis obsoletus* complex: 30 cm TL; eastern indigo snake: 45–61 cm TL; pine snake, *Pituophis melanoleucus*: 35–50 cm TL; coachwhip, *Coluber flagellum*: 30–44 cm TL; Means 2017; Krysko
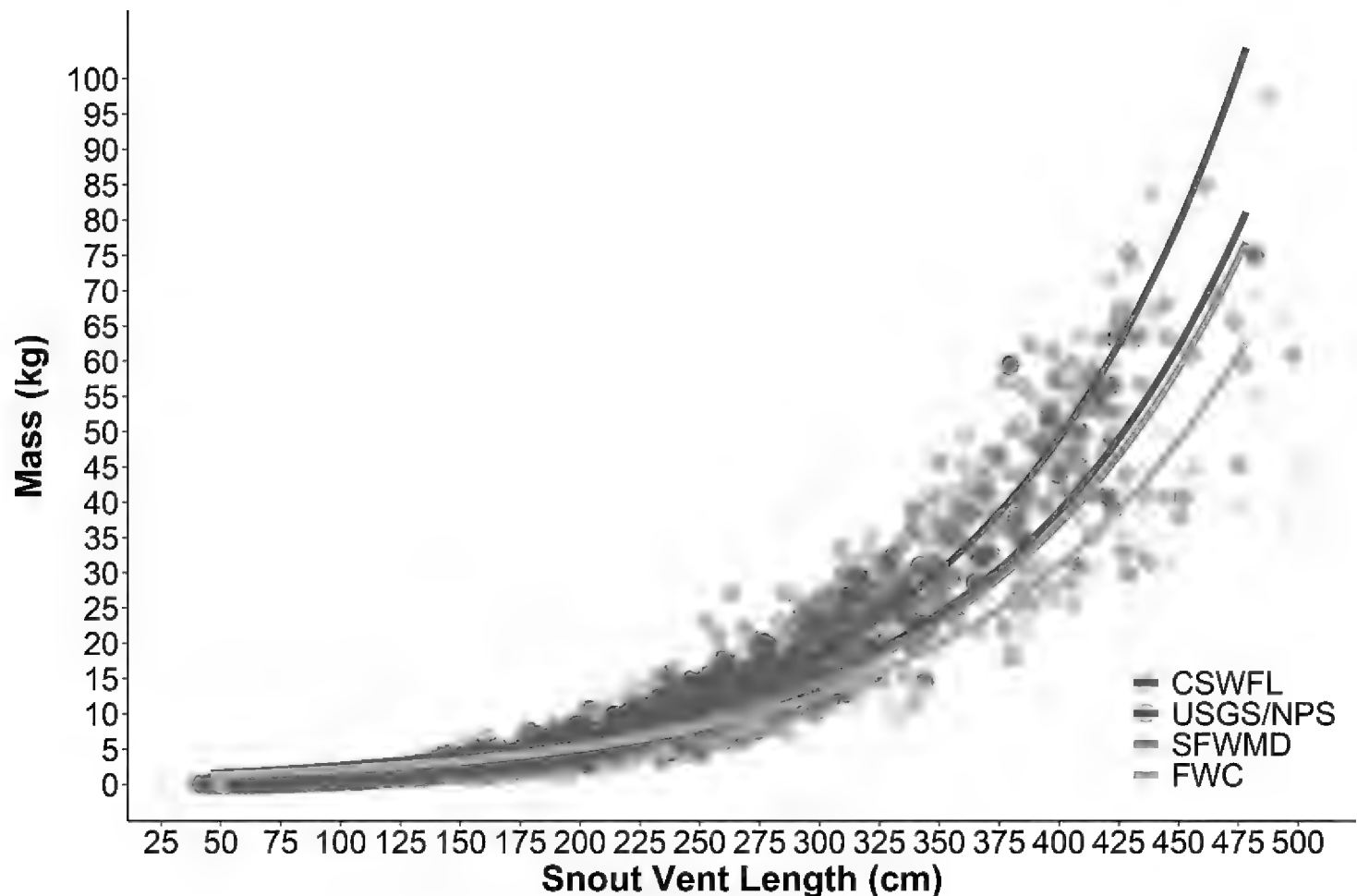
Figure 4. Relationship between snout-vent length (SVL; range: 34.44 to 500.9 cm) and mass (range 0.04 to 97.5 kg) of Burmese pythons (*Python molurus bivittatus*) measured in southern Florida, USA between 1995-2022 (n = 7,762). Data are from the U.S. Geological Survey and National Park Service (USGS/NPS, n = 3,723, Currylow et al. 2022c), Florida Fish and Wildlife Conservation Commission (FWC, n = 2,450, Suppl. material 1), South Florida Water Management District (SFWMD, n = 630, Suppl. material 1), and Conservancy of Southwest Florida (CSWFL, n = 959). Explanations for observed differences in mass-length relationships are not yet well-characterized for Burmese pythons but may be influenced by several factors (see Size Distribution section), including habitat-driven features like prey availability as well as capture method. For example, programs that predominantly use scout snakes (e.g., CSWFL) appear to result in the capture of larger, reproductive adult pythons (e.g., Smith et al. 2016) compared to pythons found during road cruising (e.g., FWC and SFWMD; see Removal Program and Scout Snake sections).

et al. 2019b). Large hatchling size may result in competitive and survival advantages over native snake species (e.g., Bonnet et al. 2000). Upon hatching, Burmese pythons retain a yolk sac in their abdomen containing lipids, proteins and other nutrients (e.g., Thompson and Speake 2003) that is eventually absorbed; the length of time this process takes is unknown but has been suggested to occur by the first ecdysis event at 2–4 weeks of age (Van Mierop and Barnard 1976b; Josimovich et al. 2021), though traces of some yolk sac materials can remain as long as a few months in snakes that eat regularly or are in good body condition (J. Josimovich, USGS, Written Communication, 07/22/2021). Although hatchling pythons do not eat during this yolk-absorption phase, and thus lose weight, they still increase in length (Van Mierop and Barnard 1976b; Josimovich et al. 2021). Mean egg and hatchling weight are variable among clutches (Vinegar 1973; Josimovich et al. 2021) and thus could be an important com-

ponent of both early survival and longer-term fitness, particularly if lifetime growth rates are shaped by the quality and frequency of feeding experiences early in life, as has been found for other python species (Madsen and Shine 2000). It is not known to what extent maternal investment in yolk varies and what factors (e.g., body condition or some heritable trait) might influence this variability.

Size at maturity

In the native range, females are considered mature at approximately 260 cm TL (~10 kg; Wall 1921; Frye and Mader 1985; Reed and Rodda 2009). In southern Florida, Willson et al. (2011) reported a monthly size distribution of female pythons including gravid snakes and suggested that females mature at 230 cm SVL, although smaller mature females with oviductal eggs have been documented (185 cm SVL, 210 cm TL, Willson et al. 2014; Currylow et al. 2022b, c; 186 cm SVL, 210 cm TL, Anderson et al. 2022). Based on seasonal size distribution data, most females are thought to mature between 24–36 months of age and produce their first clutch at 3-years-old (Willson et al. 2011, 2014). Targeted studies to determine the average age of first reproduction and the relationship between body length (related to age) and clutch size would allow completion of a life table for Burmese pythons (see Demography section).

In the native range, the smallest reproductive male of the closely related Indian python measured 172 cm SVL (198 TL; Vishnu et al. 2021). Small mature male Burmese pythons have been documented in breeding aggregations in Florida (168 cm SVL, 193 cm TL; Smith et al. 2015) and thus far, the smallest sexually mature male has measured only 125 cm SVL (143 cm TL, Currylow et al. 2022b, c).

Maximum size

As with most ectotherms, maximum size is determined by factors such as environmental conditions, available resources, resource allocation decisions, and genetic variability (Heino and Kaitala 1999; Cox and Secor 2007; Frýdlová et al. 2019; Josimovich et al. 2021), and these factors influence the maximum size that individuals in a population can attain in a specific habitat. Thus, if pythons in the Florida population experience similar environmental conditions and conform to equivalent physiological tradeoffs between reproduction and growth, most variation in python size should be attributable to a combination of python age and food availability across space and time. New record-sized pythons may continue to be discovered as efforts to find and remove pythons increase. The largest wild female pythons in Florida have been between 500 and 600 cm TL and 60–97 kg (Fig. 4; Krysko et al. 2012, 2019a; Bartoszek 2022; Currylow et al. 2022b) with the longest measuring 518 cm SVL (572 cm TL; M. Spencer, FWC, Written Communication, 7/30/2021). Reproductive adult males in Florida are mostly between 207 and 216 cm SVL (n = 138), with 400 cm SVL and 44 kg at the upper end (Currylow et al. 2022b), but this is far surpassed by the single largest documented from a breeding aggregation measuring 493 cm TL (438 cm SVL) and 63.5 kg (Easterling and Bartoszek 2019).

Growth and longevity

Somatic growth patterns are a key life-history trait in all organisms and influence maximum body size which in turn affects survival, fecundity, and competitive ability (Stearns 1989). Individual growth varies among sexes and populations because of genetic and environmental factors. Quantifying the variation in individual growth patterns, especially among growing females (i.e., the sex contributing to population abundance) can have implications for control of invasive species (e.g., age of reproductive maturity).

Growth rates of wild pythons in Florida are not well-documented, in part because encountered individuals are generally removed rather than being marked, released, and recaptured to provide information on growth during the inter-capture interval. Captive feeding studies have documented Burmese pythons growing as fast as 20 cm per month (Wall 1921; Frye and Mader 1985), but because these conditions are unlikely to be experienced by wild pythons, their growth rates in Florida are not transferable to questions related to age estimation.

In Florida, python age is only identifiable for the first several months of their first year, after which variation in individual growth makes it difficult to distinguish year classes (See Hatchling Size section). Pythons are approximately 100 cm SVL after one year (Willson et al. 2011; Falk et al. 2016). Pittman and Bartoszek (2021) measured the length of 8 wild hatchling Burmese pythons in southwest Florida over three years and found that growth rates generally peaked within the first 12 months after hatching (3.7–7.2 cm SVL/month) and declined thereafter.

Currently there are no longevity estimates for wild pythons, but the longest lifespans documented in captive Burmese pythons exceed 30 years (i.e., 28–34 yrs; Bowler 1977). Data from long-term tracking of individual pythons may inform longevity estimates. For example, one adult male python (350 cm SVL), initially radiotagged in 2013, has been consistently monitored through 2021 (500 cm SVL) and tracking is ongoing, indicating a wild lifespan of at least 10 years (I. Bartoszek, CSWFL, Written Communication, 5/27/2021). More information on longevity is particularly important to inform reproductive potential of females. Average longevity coupled with average annual fecundity and survival to reproduction can provide estimates for the contribution each surviving female may have on population growth rate.

Physiology

Wild Burmese pythons can exhibit physiological resilience to stressors, including short-term captivity and handling (Claunch et al. 2022), and in addition to basic biology, a solid understanding of their physiology may inform how this species has become such a successful invader in southern Florida.

Thermal biology

Burmese pythons are ectotherms that largely rely on environmental heat sources to control body temperature. However, they are active thermoregulators and use behav-

iors such as basking or seeking shade (Pough 1980; Stevenson 1985; Shine 2005) as well as altering body posture between outstretched and coiled positions to change heating and cooling rates (Johnson 1972). An experimental study conducted in a semi-natural enclosure in South Carolina documented thermoregulatory behaviors in Burmese pythons, including basking in the sun to increase body temperatures well above ambient air temperature, particularly during winter months of November–January (Dorcas et al. 2011). Observational field studies in southern Florida have also documented basking behavior (Mazzotti et al. 2011). Shivering thermogenesis (see Reproduction section) has not been observed in males or non-reproductive females.

Body temperature influences behavior, physiology, and development (e.g., Stevenson 1985) and is determined in part by a combination of body size and position, reflectivity, regional climate, immediate weather conditions, and microhabitat selection (Stahl et al. 2016). Although little is known about thermal physiology of wild Burmese pythons in their native range, they occur across wide range of climates and habitats (Rodda et al. 2009). Thus, in southern Florida, python physiology will be influenced by the genetic makeup (i.e., geographic origins) of the invasive population, plasticity of physiology and behavior, and capacity for rapid evolution of these traits (e.g., Card et al. 2018).

The aspect of thermal physiology most relevant to the Burmese python invasion in southern Florida is cold tolerance, with minimum temperature extremes being a stronger driver of survival than average temperature over a span of time (Avery et al. 2010). At temperatures less than 10 °C, Burmese pythons are increasingly at risk of dying from exposure (Avery et al. 2010; Dorcas et al. 2011; Mazzotti et al. 2011), and 5 °C is thought to be a conservative estimate of the critical thermal minimum (Jacobson et al. 2012) based on studies of garter snakes (*Thamnophis* spp.) in temperate regions (Doughty 1994). A critical thermal minimum for ectotherms is the low temperature at which mobility is lost; if temperatures continue to fall, the lethal thermal minimum is reached, leading to death (Cowles and Bogert 1944). However, critical thermal minima have not been determined for Burmese pythons, and large variation in body size across life stages may result in differences in critical thermal minima and cooling rates among different-sized pythons (e.g., Claunch et al. 2021). Field observations of wild Burmese pythons in southern Florida have documented mortality when air temperatures remained at or below 10 °C for at least 48 hours, culminating in lows of -4 to 0 °C (Mazzotti et al. 2011). In a semi-natural outdoor enclosure in South Carolina, 10 Burmese pythons from ENP survived overnight drops in core body temperature as low as 4 °C (Dorcas et al. 2011). However, all snakes eventually died and most deaths were associated with sustained body temperatures between 5 and 10 °C (Dorcas et al. 2011). Using a mechanistic bioenergetics model, Stahl et al. (2016) simulated Burmese python body temperatures over the range of air temperatures occurring in southern Florida during a record cold-spell (Mazzotti et al. 2011) and suggested that mortality likely occurs from an inability of pythons to generate energy at low temperatures, leading to decreased respiration rates and hypoxia (e.g., Davies and Bennett 1981), rather than formation of ice crystals within cellular spaces (Storey and Storey 1992). Necropsy results from Dorcas et al. (2011) confirmed python deaths

were caused by hypothermia rather than factors indirectly related to cold temperatures (e.g., disease, parasite load, poor body condition, or stress).

To survive lethally cold air temperatures, pythons must retreat into sheltered refugia and remain there until temperatures warm again. Thus, understanding thermoregulatory behavior is critical to projecting range expansion beyond southern Florida. Burmese pythons in northern India appear to use refugia (e.g., porcupine burrows) to escape cold winter temperatures (Bhupathy and Vijayan 1989), and there is evidence that pythons in southern Florida also use underground or aquatic refugia during cold (Mazzotti et al. 2011, Dorcas et al. 2011, I. Bartoszek, CSWFL, Written Communication, 5/17/2021). Indeed, some portion of the southern Florida population survived freezing temperatures during 2010 (Mazzotti et al. 2011) and these snakes and their offspring make up the current population. However, some Burmese pythons do not appear to have this refuge-seeking behavioral response during cold temperatures. For example, both wild pythons (Mazzotti et al. 2011) and some of those kept in outdoor enclosures have been documented attempting to bask during freezing temperatures, with some leaving heated enclosures to do so, and others employing coiled thermoregulatory body positions (Avery et al. 2010; Dorcas et al. 2011). With consideration of the maladaptive basking behaviors, Jacobson et al. (2012) examined weather data from three regions in Florida and a site in South Carolina, in conjunction with minimum temperature estimates for the lower limits of digestion (16 °C), activity (5 °C) and survival (0 °C) and concluded that it is unlikely Burmese pythons could expand to more temperate areas of Florida and adjoining states without appropriate thermoregulatory shelter-seeking behavior during cold. However, rather than pythons, these activity estimates are based on temperate North American snake species (*Thamnophis*, *Nerodia*) and are applicable to a wide range of species that seasonally vary their activity window and make use of available refugia. Further, pythons have been documented using gopher tortoise (*Gopherus polyphemus*) and nine-banded armadillo burrows (*Dasypus novemcinctus*; Bartoszek et al. 2018a, 2021b), and there is evidence for selection in genes associated with cold tolerance after undergoing a cold event (Card et al. 2018). Cold tolerance adaptation may allow the Florida population to occupy areas somewhat cooler than would be predicted by extrapolating from the areas they were sourced (see Potential Range and Energetics/Digestion sections).

Osmoregulation

High salinity has been suggested as a limiting factor affecting reptile distribution in coastal habitats because very few species have adaptations (e.g., salt glands) to regulate salt uptake (Dunson and Mazzotti 1989). Nonetheless, Burmese pythons have established in the Florida Keys (Hanslowe et al. 2018), likely through overwater dispersal from the nearby mainland. Indeed, there have been many observations of pythons swimming up to 25 km from the mainland in Florida Bay and Biscayne Bay, indicating marine dispersal is possible (Bartoszek et al. 2018c; Hanslowe et al. 2018).

Hatchling Burmese pythons provided with marine water (salinity = 35 ppt) to drink survived in the lab for approximately one-month (mean = 32 days, 95% CI 23–40),

whereas in brackish treatments (salinity = 10 ppt) pythons survived about five months (mean = 156 days, 95% CI 115–197 days; Hart et al. 2012). Notably, one juvenile python (~ 1-year-old) survived on marine water until the experiment was terminated at 200 days, and it is unclear how hatchling salinity tolerances compare to those of adult pythons (Hart et al. 2012). Hatchling pythons presumably have higher cutaneous water loss rates compared to larger individuals, but water loss may be offset by presence of yolk sacs (see Hatchling Size section). These lab experiments likely underestimate the potential of pythons to persist in saline habitats in the wild given that pythons using marine areas may still have access to freshwater sources through rainfall (Hart et al. 2012) and consumption of prey. It is unclear whether pythons in marine water treatments survived for a month by tolerating high salt loads during drinking or by reducing their water intake such that they were dehydrated, but survival in marine treatments (Hart et al. 2012) and evidence of marine dispersal (Bartoszek et al. 2018c; Hanslowe et al. 2018) suggests that salinity may not severely limit the coastal range of Burmese pythons.

Energetics and digestion

Python digestive physiology and energy budgets can be used to estimate rates of prey consumption, which are critical to understanding impacts on native species (see Diet and Prey Decline sections). Burmese pythons have unique morphological and physiological responses to feeding and fasting that likely have contributed to their success as invaders in Florida. Burmese pythons are thought to be primarily ambush predators (Reed and Rodda 2009), a strategy that presumably influenced evolutionary adaptations to accommodate large meals and long fasting intervals (Secor and Diamond 1995, 2000). The Burmese python gastrointestinal tract is downregulated between meals and does not produce acid, stopping gall bladder and pancreatic secretion, depressing activity of intestinal nutrient transporters and enzymes, and shrinking the intestinal epithelium and microvilli (reviewed in Secor 2008). The downregulation extends to atrophy of organs such as the heart, kidney, liver, and small intestine, such that fasting laboratory Burmese pythons have among the lowest basal metabolic rates among vertebrates (Secor 2008). However, within 48 hours of feeding, gut tissues rapidly secrete digestive acid and enzymes and experience extreme organ growth that coincides with the highest increase in metabolic rate documented among vertebrates (40-fold increase; Secor and Diamond 1995, 2000; Secor 2008). The high post-feeding metabolic rate of pythons is partially attributed to the need for the stomach to digest large intact prey (potentially > 100% of body mass; Bartoszek et al. 2018b) before passage to the small intestine, compared to other organisms that pre-process food by dismemberment or mastication (Secor and Diamond 1995).

An energy budget is a means of dividing ingested energy into allocations for metabolic processes and production (e.g., maintenance, growth, reproduction, fat storage) and for losses (i.e., in feces and urates; Congdon et al. 1982). Energy budgets can facilitate modeling of energy intake, growth rates, and potential reproduction of Burmese pythons in southern Florida. Cox and Secor (2007) developed a 10-day energy budget for a captive 500-g Burmese python, maintained at 30 °C, and fed a rat meal

25% of snake body mass. The authors then extended results, incorporating data from another sit-and-wait foraging species, to construct a hypothetical energy budget for a similar-size wild Burmese python (i.e., less frequent feeding, more active), noting that estimates can be improved by incorporating data on feeding frequency, meal type, meal size, body temperature, and activity (Cox and Secor 2007).

There are no rigorous estimates of feeding frequency in wild Burmese pythons, because there are little data on pythons with empty stomachs. An examination of 1,716 pythons known to have contents in their digestive tract indicated the average number found in an individual python was 1.28 prey items, although one python contained 14 cotton rats (*Sigmodon hispidus*), including nine newborn rats (C. Romagosa, UF, Written Communication, 9/21/2022). Card et al. (2018) genetically sampled Burmese pythons before and after a major freeze event in 2010 and identified a shift in genomic regions over time, with natural selection for genes linked to regenerative organ growth, and the modulation of organ size and function with feeding and fasting (Andrew et al. 2017). This shift could be associated with smaller, more frequent meals from abundant rodent populations (see Diet section). Thus, rapid adaptation among pythons in southern Florida may be the result of interactions between consistent ecological pressures, such as shifts in food availability, and acute climatic pressures associated with periodic freeze events.

Detection probability

Broadly speaking, detection probability is the chance that an individual or species will be detected during a survey, given that it is present at the site. Snakes are generally considered the most difficult reptile group to study because of low detectability, resulting from secretive behavior, cryptic coloration, low and sporadic activity, and low abundance (Steen 2010; Durso et al. 2011; Willson et al. in press). These difficulties extend to Burmese pythons, a cryptically colored species that is mostly nocturnal and spends much of its time submerged in aquatic habitats or concealed underneath vegetation or limestone bedrock (Smith et al. 2021; see Habitat Use section, Fig. 5). These individual behaviors are compounded across the vast and largely inaccessible Greater Everglades Ecosystem (see Introduction) and have resulted in extremely low visual searching or trapping detection probabilities (e.g., Dorcas and Willson 2013; Nafus et al. 2020). The difficulty of visually detecting or trapping pythons in an immense natural landscape has been one of the hallmark issues of the invasion (e.g., Reed et al. 2011; Falk et al. 2016), leading to a delay in acknowledging the establishment of the species and continuing to hamper our ability to conduct and evaluate control efforts. Very low individual detection probabilities for Burmese pythons remain the key obstacle to deriving reliable population estimates and developing landscape-scale control programs.

Types of detection probability

There are two types of detection probabilities to consider depending on research or management goals: detection at the level of the 'species' or the 'individual'. Species de-

tection probability is used in occupancy studies and refers to the probability of directly or indirectly (e.g., from tracks or environmental DNA [eDNA]) encountering at least one individual of that species in a given area, given that at least one individual truly occupies the area. Individual detection probability, typically derived from capture-mark-recapture studies, refers to the probability of detecting a particular individual snake (Williams et al. 2002). Individual and species detection are related; if individual detection (p) can be known or assumed, the probability of detecting at least 1 of the n individuals in a population during a single survey is: $1-(1-p)^n$. Importantly, detection probability of both types is not fixed, but instead is a function of the behavior of the target species (e.g., activity increases during the breeding season), efficacy of the capture method and/or observer, degree of effort expended, and survey conditions such as weather, season, and habitat type (Lebreton et al. 1992; Tyrrell et al. 2009; Christy et al. 2010; Willson et al. in press).

Species detection

The distinction between species and individual detection is important because species detectability reflects both abundance (i.e., how many individuals are present) and individual detection probability (i.e., how difficult each individual is to find). For example, species detection at a site may be considered high because an abundant species is detected on a large proportion of surveys, yet most individuals themselves will rarely be detected because of low individual detection probabilities. Understanding species detectability is critical for determining the geographic extent of an invasion, tracking spread, developing early-detection/rapid-response protocols, and assessing eradication status. Species detectability is generally used to determine whether a species is present at a given location and is frequently estimated at a population level using hierarchical models such as occupancy models (e.g., Pavlacky et al. 2012; Bailey et al. 2014) that account for imperfect detection. Imperfect detection occurs when a species is present, but may go undetected during a portion of surveys due to the challenge of detecting wild animals or the survey sensitivity, which can result in biased occupancy estimates (MacKenzie et al. 2002, 2017; Tyre et al. 2003). Notably, in an occupancy framework, species with low detection probabilities may require numerous surveys to reliably confirm absence (Kéry 2002; Durso et al. 2011; Sewell et al. 2012; Steen et al. 2012). For example, to reliably declare absence of rainbow snakes (*Farancia erytrogramma*), a semi-aquatic snake species with low species detection probability (p = 10%), 27 surveys (>810 trap-nights) were required (Durso et al. 2011).

Environmental DNA as a detection tool for pythons

Environmental DNA is DNA released from an organism into the environment through sources such as feces, mucous, shed skin, hair, or decomposing carcasses (Lodge 2010). Typically, eDNA is detected using water or soil samples, although air samples, swabs of depredated prey items, and mosquito blood meals have been used (Rees et al. 2014; McCleery et al. 2015; Reeves et al. 2018). Environmental DNA can assist with early

Figure 5. Examples of cryptic coloration contributing to low detection probability in representative habitat where Burmese pythons (*Python molurus bivittatus*) have been captured. White circles indicate pythons. Photographs illustrate python crypsis in hammocks (**a–c**), shrubs, mangroves, trees, (**c, g, h**) and cypress domes and wet prairies (**d, e, f**). Photo credits: Crocodile Lake National Wildlife Refuge (**a, b, h**) and U.S. Geological Survey (**c–g**).

detection of invasive aquatic, semi-aquatic, or terrestrial animals across the landscape or to evaluate removal efforts within strategic areas (Ficetola et al. 2008; Jerde et al. 2011; Takahara et al. 2013; Miralles et al. 2016; Hunter et al. 2019).

Burmese python eDNA can be successfully amplified from water (Piaggio et al. 2014; Hunter et al. 2015) and soil (Kucherenko et al. 2018) samples that have been exposed to pythons in the laboratory or wild. In an experiment where captive Burmese pythons were submerged in water and then removed, eDNA was detected using traditional polymerase chain reaction (PCR) for up to 96 hours (Piaggio et al. 2014). Subsequently, eDNA field trials in southern Florida successfully detected tracked radiotagged Burmese pythons at locations without knowledge of python presence (Hunter et al. 2015, 2019; Orzechowski et al. 2019a).

Because the Greater Everglades Ecosystem in Florida is a vast, shallow marsh with slow laminar sheet flow, eDNA monitoring has been efficient for species detection of Burmese pythons as compared to other tools such as visual searches, trapping, telemetry, or cameras (e.g., visual survey efforts resulted in <0.05 detection probabilities (Nafus et al. 2020). Hunter et al. (2015) surveyed 21 locations distributed across southern Florida and detected Burmese python eDNA in 37 of 63 water samples using quantitative PCR. Applying a three-level eDNA occupancy model, the authors estimated cumulative probability of detecting python eDNA ranged from 0.91 to 1.00, suggesting that three quantitative replicates per eDNA sample were sufficient to detect python eDNA when it was present in a sample (Hunter et al. 2015). Importantly, cumulative detection over three samples translates to a per-sample detection probability (p) of 0.55 for any one of the three samples (Hunter et al. 2015; see Detection section; $1-(1-p)^3 = 0.91$). Conditional detection probabilities (in each PCR replicate) ranged from 0.59–0.87 and occurrence probabilities ranged between 0.57 and 0.80. Next, Hunter et al. (2019) examined Burmese python range distribution in the northern Everglades, in and south of LNWR (Fig. 1) by collecting water samples from 87 sites and analyzing them using digital droplet PCR. Python eDNA was detected at LNWR consistently across all years of the study (2014–2016) despite a lack of visual sightings. Using a site occupancy model, the conditional probability of detecting eDNA, given that eDNA is present at a site, varied from 0.38 to 0.70 (Hunter et al. 2019). Similarly, Orzechowski et al. (2019a) used a site occupancy model and documented increased python eDNA occupancy in wading bird rookeries compared to tree islands without rookeries in the central Everglades (Water Conservation Area [WCA] 3, Fig. 1). Conditional detection probability of python eDNA varied from 0.40 to 0.82 (Orzechowski et al. 2019a). Overall, conditional detection probability of Burmese python DNA in water samples using these eDNA assays is higher than visual and trapping survey techniques and relatively consistent across studies and PCR platforms, varying from 0.38 to 0.82 (Hunter et al. 2015, 2019; Orzechowski et al. 2019a; see Early Detection using eDNA section).

While eDNA is typically taken from water, it can also be amplified from soil samples for terrestrial detection of snakes. A laboratory experiment with captive bred corn snakes (*Pantherophis guttatus*) kept in terrestrial enclosures successfully identified eDNA in the soil for up to 96 hours post-removal (Kucherenko et al. 2018) and this detection window may apply to Burmese pythons. In another study, Katz et al. (Katz et al.

2021) detected Louisiana pinesnake (*Pituophis ruthveni*) eDNA in soil collected up to 25 days after telemetry confirmation. Kucherenko et al. (2018) explored the potential to detect eDNA in soil samples collected from three gopher tortoise burrows known to contain Burmese pythons. Samples were collected within 1 week of confirmed python occupancy of three burrows, and python eDNA was detected in two of three burrows (66.7%). Samples were collected from inside the burrow (1 m from the burrow entrance) rather than on the apron where DNA presumably degrades faster due to UV and heat exposure (Kucherenko et al. 2018). An additional 40 tortoise burrows with unknown occupancy were sampled in an area potentially used by Burmese pythons, but eDNA was not detected, nor were pythons seen via burrow cameras (Kucherenko et al. 2018). A lack of eDNA in these 40 burrows could indicate absence of pythons or that available eDNA was degraded or undetectable. Alternatively, pythons may have stayed within burrows for less than the amount of time required to leave detectable eDNA (Kucherenko et al. 2018). Importantly, sample size of python-occupied burrows examined by Kucherenko et al. (2018) was very low (n = 3), thus, further research is needed to establish baseline detectability using soil samples when pythons are known to be present. Similarly, Burmese python DNA has been detected in blood meals of several mosquito species (Reeves et al. 2018) and represents an alternative approach for early detection using eDNA; however, this method requires corroboration from field studies.

Overall, eDNA is useful as a detection tool for cryptic species in that it does not rely on visual observations, utilizes readily available environmental samples and is not harmful to the environment or local species (Smart et al. 2015). Thus, eDNA sampling of aquatic areas can help to inform the python population boundary where visual observations are unlikely, or to identify python eDNA presence after removal efforts. However, translating eDNA detections into Burmese python captures is unlikely with the current technology. While eDNA can facilitate early detection, by indicating the presence of a python in an area, it cannot pinpoint an exact location that would result in a capture. Future work using new technology with cost-effective on-site instruments could help to rapidly track eDNA upstream to its source or identify areas with high concentration of eDNA to target for search efforts.

Challenges with eDNA

Although use of eDNA can minimize some aspects of labor-intensive traditional surveys (e.g., capture mark recapture, visual surveys) and thereby increase the ability to detect species, several challenges remain when using eDNA (reviewed by Beng and Corlett 2020). The eDNA released by aquatic or terrestrial organisms into water is not necessarily concentrated at the site of its release, but is transported across space (e.g., downstream) and dispersed and degraded over time (reviewed by Harrison et al. 2019). Transport of eDNA could lead to detections in locations where the species is absent (Moyer et al. 2014; Beng and Corlett 2020). Degradation of eDNA from warm, humid, and acidic conditions can result in false negative detections and thus it is possible for eDNA of a target species to be absent in samples collected from a location where the species is present (Beng and Corlett 2020). Because detection of any species is

rarely perfect or constant (see Detection section), false negatives exacerbate imperfect detection and can result in an underestimation of a species' distribution. Methods to handle imperfect detection include site occupancy models which rely on repeated surveys to account for imperfect detection, with careful consideration of the study design and appropriate number of replicate samples per site and replicate amplifications per DNA sample (Schmidt et al. 2013; Hunter et al. 2015; Guillera-Arroita et al. 2017; Dorazio and Erickson 2018).

Individual detection

For other management related questions (e.g., estimating abundance change over time), knowledge of individual detection probability is critical as it influences assessment of effective control strategies. A comprehensive understanding of individual detection probability has been a cornerstone of management initiatives for another invasive snake, the brown treesnake (*Boiga irregularis*) on the island of Guam (Gragg et al. 2007; Rodda et al. 2007; Tyrrell et al. 2009; Christy et al. 2010; Yackel Adams et al. 2018). Because individual detection probability reflects the probability of detecting a particular individual per unit of search effort, it is not directly influenced by abundance, and it is generally much lower than species detection probability. Thus, estimation of individual detection probability typically requires intensive effort (e.g., repeated capture-mark-recapture surveys; Lebreton et al. 1992). Thus far, mark-recapture studies of Burmese pythons in southern Florida have been limited by logistical challenges (see below) as well as local permitting restrictions on releasing captured individuals back into the wild after each survey. Yet, mark-recapture remains the current gold standard for monitoring wild animal populations (Pollock 1976; Otis et al. 1978; Cam 2009). Accurate techniques for estimation of population size or the effect of removal efforts when detection probabilities are close to 0 are vital, such as novel development of population estimation techniques that are better equipped to handle very low visual/individual detection probabilities, low rates of removal, or improve detection for cryptic reptiles (Nafus et al. 2020; see Abundance section).

Individual detection probability of Burmese pythons is extremely low. Using data from 59 visual surveys (144 person-surveys) for wild pythons along the C-110 canal near the Frog Pond Wildlife Management Area (Frog Pond WMA; Fig. 1), individual detection has been estimated at between 0.01–1.46% per survey, with an overall expectation that detection is less than 5% and varies with the number of observers and time of day (Nafus et al. 2020). Likewise, estimates of individual detectability of 10 radio-tagged, wild-caught, male Burmese pythons in a semi-natural outdoor enclosure (31 × 25 m) indicated that detection probability during pedestrian surveys was less than 1%, even in a confined, artificial environment (Dorcas and Willson 2013). In this study, pythons were frequently undetectable to observers because they were underwater or underground, but in some cases snakes were missed even when they were in highly visible locations (Dorcas and Willson 2013). Low detectability of Burmese pythons is attributed to their cryptic coloration and secretive behavior and is exacerbated by

microhabitat selection that includes use of trees and dense vegetation, underground refugia, and water (see Habitat Use section), and their adaptations to infrequent feeding which facilitates low activity (Secor 2008; Castoe et al. 2013; Siers et al. 2018). Further, low detectability of pythons is influenced by difficulty humans have in accessing densely vegetated and/or seasonally flooded habitats in southern Florida, thus pythons have essentially zero detectability unless they are in limited areas that can be searched (see Visual and Road Survey section).

Low detection probability is a major challenge to python research and management because many surveys are needed to detect and remove most individuals within a population. In addition, estimation of demographic parameters such as abundance, survival, and recruitment (used to inform management) also generally depend on repeated detection of individuals over the course of many surveys that may span months or years (i.e., capture-mark-recapture; Williams et al. 2002; Steen 2010; Willson et al. 2018; Willson et al. in press). In addition, low and/or variable detection probabilities can induce bias in the models used to analyze mark-recapture data (Pollock et al. 1990). Similarly, other methods that provide population size and survival estimates, such as distance sampling or N-mixture models for abundance estimation, may have limited efficacy for snakes (Rodda and Campbell 2002; Ward et al. 2017) because problems with low detection are amplified compared to traditional mark-recapture approaches. Further, problems with low detection probability are compounded by factors that lead to unmodeled variation (i.e., heterogeneity) in detection such as survey type, season, habitat, size, and sex. For example, visual detection of brown treesnakes varies with weather, body condition, and observer, but also by sex, with both small and large females having lower detection probabilities than males of those sizes (Christy et al. 2010). Because of mate-seeking behaviors (see Movement section), male Burmese pythons may have different movement patterns than females (Hart et al. 2015; Smith et al. 2016; Bartoszek et al. 2021b) which may result in higher detection of males. Likewise, there is variation in detectability depending on capture methods. For example, whereas surveys that use radiotagged snakes to locate untagged snakes (e.g., scout snakes; Fitzgerald et al. 2021) can yield higher numbers of large, reproductive females (Krysko et al. 2012; Smith et al. 2016; Bartoszek et al. 2021b), road-cruising captures can produce many juvenile pythons, particularly June through September when hatchlings disperse, as well as small adult pythons (Smith et al. 2016; Falk et al. 2016; see Size Distribution section).

Burmese python arrival in Florida

History of imports into the USA

Burmese pythons have been among the most heavily traded snake species for many decades (Hierink et al. 2020). They were historically traded for their skin, and although have been kept as pets since at least the early 1900s, Burmese python popularity in the pet

trade greatly increased by the 1970s (Reed and Rodda 2009, Romagosa 2014). Beginning in 1975, export and import of certain animal and plant species began to be monitored by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which now partly regulates the legal international trade of certain snake species, including the Burmese python and all other giant constrictors, to ensure international trade is sustainable, legal, and traceable (CITES 2020; Hierink et al. 2020).

Although the CITES import records are the best available metric of international trade, import records are unreliable (e.g., potential cross-border smuggling for subsequent re-export; Blundell and Mascia 2005), making it challenging to accurately interpret declared volumes of trade. Nevertheless, according to the CITES Trade Database, from the late-1970s until 1994, live Burmese and Indian pythons (*P. bivittatus*, n = 127,356; and *P. molurus*, n = 6,100; see Taxonomy section) were imported into the United States, and most originated from Thailand (56%, n = 68,892) followed by Myanmar (33%, n = 44,573; CITES 2020). Then, from 1994 to 2011 the majority of imported Burmese pythons to the United States were from Vietnam (96%, n = 160,655; CITES 2020), in part because Thailand began to enforce the protected status of their declining python populations (Hoover 1998; see Native Range section). In some years, Burmese python exports from the United States outnumbered imports. In 1993, for example, 139 pythons were imported to the United States compared to the 591 that were exported (Hoover 1998), indicating a robust trade in captive-bred snakes. Commercial imports to the United States stopped in March 2012 when the Burmese python was added to the injurious species provision of the Lacey Act (Fish and Wildlife Service 2015), a law created in 1900 to address illegal wildlife trade, protect species at risk, and bar international importation of injurious species unless otherwise authorized by the U.S. Fish and Wildlife Service (USFWS; Hoover 1998; Jewell 2020). In 2008, the Florida Fish and Wildlife Conservation Commission (FWC) implemented regulations on Burmese pythons in Florida, adding them to a Reptiles of Concern list requiring people in possession of a Burmese python to obtain a license. Burmese pythons were then further regulated by the FWC as a Conditional species in 2010 and then as a Prohibited species in 2021 (Chapter 68-5, Florida Administrative Code), which further limited possession of the species in the state to qualifying entities engaged in research, public exhibition or for the purposes of eradication/control of wild Burmese pythons.

History of the invasive Florida population

Reports of escaped pet Burmese pythons in the United States have occurred since at least the early 1900s (Conant 1938), and an early record of a python in the Everglades dates back to 1912 (Tampa Daily Times, 8 July, 1912). A road-killed adult Burmese python measuring 3.58 m was collected on US-41 (the northern boundary of ENP) in 1979 (Fig. 6, Snow et al. 2007a). Following that, there are no confirmed reports in the Everglades for many years, despite thorough research describing non-native reptiles and amphibians of Florida (Wilson and Porras 1983; Butterfield et al. 1997). Unconfirmed reports from ENP personnel indicate observations of Burmese pythons dating back to the 1980s in the southwestern part of ENP and mangrove areas (Fig. 1;

Meshaka et al. 2000); however, records of these observations could not be located in the National Park Service (NPS) data repository of the South Florida Collections Management Center for Everglades National Park (J. Ketterlin, USFWS, Written Communication, 9/19/2022). The first two Burmese pythons documented inside ENP were collected from Main Park Road near West Lake (hatchling: 64 cm SVL, adult: 212 cm SVL) in December 1995 (Fig. 1, Snow et al. 2007a; EDDMapS 2018; Currylow et al. 2022c). Burmese pythons have since been observed in ENP every year since 1995, with 11 pythons (4 observed, 7 removed) between 1995 and 2000. Most of these individuals (n = 8) were from the southwestern portion of ENP in the saline glades and mangrove swamps near Flamingo and West Lake (Snow et al. 2007a; Figs 1, 6). However, three observations were from locations ~30–65 km north of Flamingo, including one record in 1996 of a Burmese python (191 cm SVL) in the East Everglades Expansion Area near Chekika, another (288 cm SVL) in 1997 at Paradise Key near Royal Palm, and a third in 1998 near the intersection of Pa-hay-okee and Main Park Roads (Fig. 1; Suppl. material 2, EDDMapS 2018; Currylow et al. 2022c). Together, these observations suggest that multiple generations of Burmese pythons were present in ENP by 2000 or earlier and that the population occupied a large geographic area. Burmese pythons were documented as established in Florida for the first time in the literature in 2000, and were considered to represent an established reproducing population at the time due to presence of multiple size classes observed over several years in multiple areas (Meshaka et al. 2000). The time lag between initial observations and the recognition of their establishment was largely a result of assumptions that individual pythons were isolated releases or escapes, compounded by the extremely low individual detection probability for these snakes (see Detection section).

Between 2001 and 2003, many more Burmese pythons were documented throughout ENP, including from the Long Pine Key and Hole-in-the-Donut regions in the central part of the Park, the Chekika region on the eastern boundary of the Park, and the US-41, L-67, and Shark Valley regions in the northwest part of the Park (Figs 1, 6; Snow et al. 2007a; Falk et al. 2016; EDDMapS 2018; Currylow et al. 2022c). Records from 2004–2006 expanded the invasive range farther north to include much of Big Cypress National Preserve and regions east along I-75 (Fig. 1; Falk et al. 2016). Notably, the first Burmese python record at I-75 (~19 km west of US-27, 42 km north of ENP) occurred in 2004, in the Everglades and Francis S. Taylor Wildlife Management Area (EDDMapS 2018). From 2007–2010, records indicate further expansion west of SR-29, northward into Palm Beach County, and east of SR-27 to include much of Broward County (Reichert et al. 2017; Figs 1, 6). The first record of a Burmese python with eggs at US-41 occurred in 2012, approximately two km east of Loop Rd (CR-94) in the Everglades and Francis S. Taylor Wildlife Management Area, and the first record of a python with eggs at I-75 (~54 km west of US-27) was in 2015 (EDDMapS 2018). The first recorded hatchling at US-41 (~23 km west of Hwy-29) was a road-killed male in 2009 (EDDMapS 2018). Hatchlings were first observed along US-41 outside of Naples in 2011 (Andreadis 2011). Pythons are now established on Key Largo (Hanslowe et al. 2018) in the upper Florida Keys, which represents the southern boundary of their current established range, and there are many records from

mangrove islands in Florida Bay and Biscayne Bay (Hanslowe et al. 2018; Bartoszek et al. 2018c). Many individuals have been found along the western outskirts of Miami, farther northwest in Big Cypress National Preserve, along Florida's west coast in Naples (e.g., CSSP, PSSF, RBNERR; Table 1, Fig. 6), and in the vast marshes north of I-75 (Figs 1, 5; Snow et al. 2007a; Mazzotti et al. 2011, 2016; McCleery et al. 2015; Bonneau et al. 2016; Reichert et al. 2017; Bartoszek et al. 2021b; Currylow et al. 2022b). There are now many records north of I-75 including agricultural areas near Lake Okeechobee (EDDMapS 2018, Fig. 6) and within the LNWR in Palm Beach County, south and east of Lake Okeechobee (Fig. 6, Table 1). The LNWR represents the minimal northern range limit of the species based on eDNA detections and a confirmed sighting of a Burmese python in the refuge in 2016 (EDDMapS 2018; Hunter et al. 2019; see Current Range section). Isolated individuals may be found well outside these areas, but the exact northern extent of the wild Burmese python population in southern Florida is difficult to determine because of challenges in distinguishing wild pythons from recently escaped or released captive animals as well as their cryptic nature and low detectability (i.e., pythons will rarely, if ever, be observed when their population density is low; see Detection section). However, by surveying a large sample of captive pythons imported from across a range of locations, years, and breeding groups, genetic tools such as multi-locus markers may help distinguish recently released pythons from wild snakes and better focus management efforts.

Introduction scenarios

Primary introduction

The initial source of Burmese pythons in southern Florida was the result of intentional or unintentional releases of captive pythons, and consideration of how they became established can be valuable for preventing establishment of similar species in the future. Willson et al. (2011) used information on python capture rates and biologically-derived population growth models to evaluate the plausibility of various scenarios for python establishment in ENP. The authors determined that a scenario involving a relatively recent establishment after 1990 would have required large numbers (i.e., 100–1,000) of founders or unrealistically high juvenile survivorship (Willson et al. 2011). Intentional simultaneous release of large numbers of pythons is unlikely given the high value of these snakes at the time and lack of motivation for a large-scale release. Willson et al. (2011) indicated that the accidental release (e.g., from Hurricane Andrew in 1992 or other natural disasters) of large numbers of founders from reptile breeder/importer facilities in southern Florida was inconsistent with the spatial and temporal pattern of python captures in the region described by Snow et al. (2007c). Therefore, the most plausible scenario for establishment of pythons in southern Florida is from an initial release of a relatively small number of adult or juvenile pet pythons in the mangrove regions of ENP near Flamingo prior to 1985 (Willson et al. 2011).
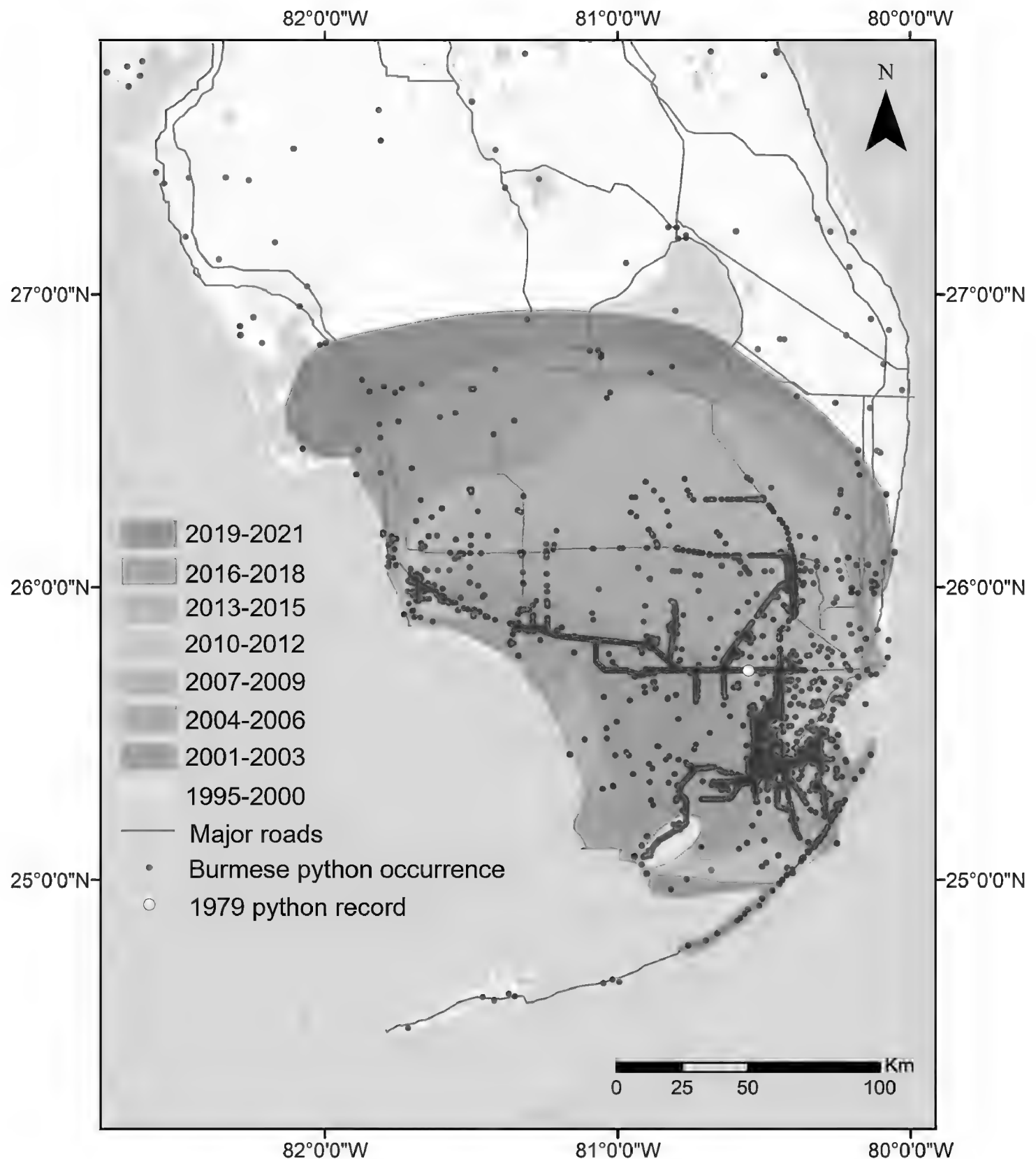
Figure 6. Geographic spread of Burmese python (*Python molurus bivittatus*) records in southern Florida between 1979 and 2021. Occurrence records were obtained from a large geospatial database of invasive species reports (Early Detection & Distribution Mapping System, EDDMapS 2018) submitted by both researchers and the public. Records are classified as 'verified', 'credible', or 'possible', and colored polygons for each timespan are general estimates delineated using the highest densities of verified records. Polygons from 1995 through 2009 are modified from Dorcas and Willson 2011. Thus far, verified records north of Lake Okeechobee cannot be confidently attributed to the southern Florida population and may represent newly escaped individuals. The area represented by the outer polygon (2019–2021) encompasses all other polygons and represents an area of approximately 29,900 km². The purpose of this map is to illustrate the chronology of python removals across southern Florida and represents the best professional estimate of the invasion front, which is not exact and will change over time.

Possible secondary introduction

There are several lines of evidence suggesting a possible second introduction of Burmese pythons to southwestern Florida. Burmese pythons were seen in the area outside of Naples and along US-41 by credible observers beginning in the late 80s and into the 90s (I. Bartoszek, CSWFL, Written Communication, 5/27/2021). The first Burmese python records in southwestern Florida occurred in 2003 and 2005, in western Collier County, near Everglades City, approximately 5 and 22 km east, respectively, of the intersection of US-41 and Hwy-29 (Fig. 1; EDDMapS 2018). During this time, from 1995–2005, all other Burmese python records were substantially farther east (~ 55 km east, along US-41) of these first two southwest Florida python observations (Fig. 6; EDDMapS 2018). Notably, Bartoszek et al. (2020) describe several observations of aberrantly patterned neonate and adult Burmese pythons captured from Collier County between 2012 and 2018; these pythons had irregular, maze-like dorsal pattern consistent with a "labyrinth" morph (i.e., snake bred for a unique color or pattern) introduced to the commercial pet trade in 1989 (Clark 1996). No labyrinth morphs have been recorded in southeastern Florida where Burmese pythons were initially introduced (see Introduction Scenarios section). It is possible that pythons with alleles for the labyrinth phenotype were introduced separately into an existing population of wild-type Burmese pythons in southwest Florida (Bartoszek et al. 2020). Alternatively, a separate introduction of Burmese pythons containing the recessive labyrinth trait may have occurred in the mid- to late-1990s in southwestern Florida, before the other population of pythons had spread from the eastern Everglades region (Bartoszek et al. 2020). A second introduction in this area is consistent with, but weakly supported by the population structure inferred by microsatellites. More specifically, the Florida population was assigned to two clusters, with most pythons in southwestern Florida assigned to the second cluster, although remaining pythons assigned to that cluster occur throughout the sampling area of the occupied range (Hunter et al. 2018). Further, recent surveys for a snake-specific serpentovirus among wild pythons in Florida have documented genetically distinct variants of the virus in southwestern Florida compared to the rest of southern Florida (see Parasites and Pathogens section). Taken together, the timing of visual observations along with information on phenotypes, genetics, and pathogens indicate that a secondary introduction of Burmese pythons to southwestern Florida may have occurred.

Population genetics

The earliest population genetics work examined 156 individual wild Burmese pythons collected in ENP between 2003–2006 and compared them to a single shed skin from a local pet store and 13 skins from a local reptile dealer that were purportedly from a wild population in Vietnam (Collins et al. 2008). Limited genetic structure was found across 10 microsatellite loci in a sample of 156 pythons collected from ENP and within one mitochondrial locus in a subsample of 16 pythons, but it was unclear whether

this finding was due to a truly panmictic population, low diversity in the pet trade, or founding effects of a single introduction. To facilitate a higher-resolution assessment of the invasive population in ENP, Hunter and Hart (2013) developed population-derived microsatellites which were combined with cross-species markers tested by Collins et al. (2008) to form eight multiplexes made up of 24 markers. These markers, along with three mitochondrial DNA loci, were then analyzed on 426 pythons from across southern Florida. Using the developed nuclear markers, two genetically diverse groups containing admixed individuals were identified, though the groups did not correlate strongly with any geographic or demographic pattern. Mitochondrial diversity did not appear to follow any geographic patterns, but two of the six mitochondrial DNA sequences were identified as originating from the Indian python sub-species (see Taxonomy section) and were more predominately associated with the second nuclear group (Hunter et al. 2018). The identified genetic diversity among pythons in southern Florida is low compared to pythons in the native range, which have nearly twice the number of alleles and higher average heterozygosity (Hunter et al. 2018). More specifically, effective population sizes were relatively small in the invasive population (Hunter et al. 2018), supporting the hypothesis that the population was established by a small number of founders, or closely related individuals, or both (Willson et al. 2011; see Introduction Scenarios section). Although allelic diversity is likely to remain low, the large (and growing) population size combined with multiple paternity (Skelton et al. 2021), and the potential of additional introductions of snakes with novel alleles, is likely to lead to increased relative genotypic diversity (Hunter et al. 2018).

Status of the Florida population

Abundance

Estimating abundance and population growth rates of wild python populations is vital for effective management, but it is difficult to obtain accurate estimates, particularly for cryptic invasive species. Although unsubstantiated ranges of abundance are frequently circulated in the popular media, there are no reliable estimates of python abundance or density. This knowledge gap makes it challenging to evaluate effectiveness of current or proposed control methods and management initiatives. A common method for abundance estimation is using capture-mark-recapture (CMR) surveys where many individuals are marked and released, and the proportion of marked individuals recaptured later can provide robust estimates of population size (e.g., Lebreton et al. 1992; White and Burnham 1999; Williams et al. 2002). However, because individual detection probability of Burmese pythons is extremely low and detection is influenced by many factors (see Individual Detection section), a python CMR study would require high levels of effort, a large amount of data to account for heterogeneity in capture probabilities, and consistent commitment of financial resources to obtain reliable and sufficiently precise estimates.

Challenges interpreting removal data

Although less rigorous, annual removal data (raw counts) can provide an approximate index of relative abundance for given areas. Falk et al. (2016) compiled 1,412 Burmese Python records from ENP during 2000–2014 and documented variation in annual observations. However, interpreting python abundance from unmodelled removal data is complicated by many factors, including detection probability, changes in effort, observer bias (e.g., Harvey et al. 2015), relatively limited search areas along roads (see Removal Programs section, Fig. 7), and potential variation in factors such as resources, habitat, and environmental conditions. Furthermore, capture rates are likely to be a function of abundance itself (i.e., human removers likely have a non-linear removal relationship to python density). As a result, removal data may not provide unbiased estimators of abundance or population size. For example, removal data for ENP peaked during 2014 which could indicate population growth, or be a reflection of increased search effort that year by a few individuals (Falk et al. 2016). Other metrics, such as catch per unit effort (CPUE), have been used to assess removal effort of invasive iguanas (Avery et al. 2014). However, the low detection probability of Burmese pythons results in high variance in the number of pythons observed, which complicates the relationship between removal rate and population size. In addition to the low precision of estimates, the mean capture rate of pythons during a survey will not only be a function of effort but also influenced by python density, observer skill, and environmental conditions and may therefore be difficult to interpret.

Records from ENP are consistent with a population decline and subsequent growth following an extreme cold event in January 2010. Python removals from Main Park Road in ENP from 2000–2014 increased dramatically from less than 10 per year in 2000 and 2001, to a peak of ~140 per year in 2009 (Falk et al. 2016). Removals then declined through 2012 (~30/y) and increased in 2013, when many young pythons were documented, and increased again in 2014 to reach the level of removals in 2009 (Falk et al. 2016). Though consistent with a population bottleneck associated with the 2010 cold event, the data are not effort-corrected, so alternative hypotheses for that pattern cannot be rejected (Falk et al. 2016). Generally, interpretation of removal data without explicit consideration of search effort can lead to spurious conclusions and counts alone are typically inadequate for estimating abundance (White 2005). Nonetheless, Willson and Pittman (2017) conducted effort-corrected road surveys along Main Park Road and documented a dramatic drop in python encounters following 2010, with minor recovery through 2017, which is concurrent with Falk et al. (2016) and the idea that the population recovered after a dieback in 2010.

An important component of Burmese python ecology is an understanding of the interactive effects of removals and natural mortality (Boyce et al. 1999), particularly whether removal mortality is additive to natural mortality rates, or whether density-dependent changes in reproduction, immigration, movement, or increased survival can compensate for losses incurred from removals (e.g., Burnham and Anderson 1984; Lebreton 2005; Zipkin et al. 2008; see Demography section). Without careful, pop-
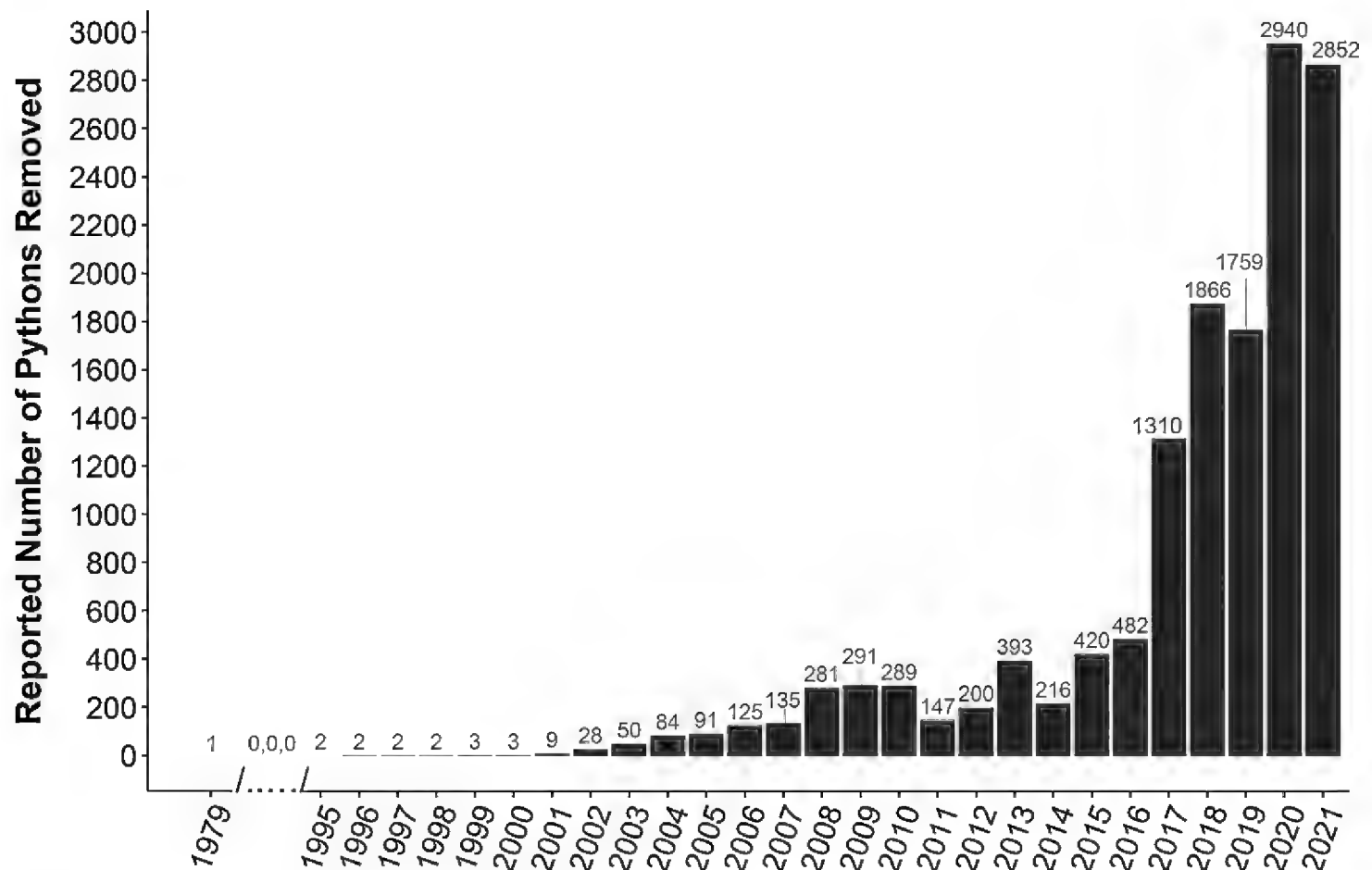
Figure 7. Annual number of reported removals of Burmese pythons (*Python molurus bivittatus*) across southern Florida through December 31st, 2021 (n=13,746). Data reported to and managed by Florida Fish and Wildlife Conservation Commission (FWC; Suppl. material 2). Pythons are predominantly removed from areas within a kilometer of a road (Fig. 6). Black bars represent the number of pythons removed through several avenues including the Florida Python Challenge, EDDMapS, State and Federal Agencies, and the FWC and South Florida Water Management District (SFWMD) paid Contractor Programs, initiated in 2017. No pythons were recorded from 1980 to 1994, as indicated by the repeating zeros on the x-axis. Overall, interpreting python abundance from unmodelled removal data is complicated by many factors, including detection probability, changes in effort, limited search areas along roads (e.g., Figs 1, 3), and potential variation in factors such as resources, habitat, and environmental conditions. Without careful population-level monitoring with baseline abundance estimates it is difficult to quantify how effective removals are, or whether removals may unintentionally result in an increase in python population abundance (see Challenges Interpreting Removal Data and Removal Programs sections). Future research goals may seek to incorporate methods to generate baseline abundance estimates (see Future Research section).

ulation-level monitoring with baseline abundance estimates, it is difficult to quantify how effective removals are, or whether removals may unintentionally result in an increase in python population abundance (i.e., overcompensation; Zipkin et al. 2009). Several empirical ecological studies of plants (Buckley et al. 2001; Pardini et al. 2009), insects (Nicholson 1957; Moe et al. 2002), and fish (Zipkin et al. 2008) have demonstrated how increased mortality of target individuals in a population resulted in greater overall abundances of the target species, and this may have important implications for predicting the outcome of Burmese python management actions. For example, a seven-year removal of over 50,000 smallmouth bass in a closed population led to higher estimated abundances, primarily because of an increase in juveniles, an age class

with high survival, but also because of the high fecundity of adults (Zipkin et al. 2008). Research has suggested that species most likely to respond undesirably to harvest/removals are those with high per-capita fecundity over discrete breeding periods, short juvenile stages, and relatively constant survivorship rates (Zipkin et al. 2009). Given high fecundity and presumably high adult survival (see Survival section) of Burmese pythons, removals may result in more resources (e.g., prey, refugia) available to remaining pythons, increasing the fitness and survival probability of snakes who might otherwise have died, grown more slowly, and/or produced fewer offspring. Finally, even if compensatory mortality does not occur among some python subpopulations (i.e., overcompensation), declining captures in previously high-density areas may result in shifts in search effort to other areas (e.g., Pasko and Goldberg 2014; Sorice and Donlan 2015; see Removal Programs section, Fig. 7) that could allow for population recovery. Therefore, without maintaining at least the same degree of removal pressure over time, the python population may continue to increase. Further, FWC and South Florida Water Management District (SFWMD) implemented paid removal programs in 2017 (see Removal Programs section) and have since expanded the number of both program participants and search areas. Although the number of pythons removed across southern Florida also increased during this time (Fig. 7), it is impossible to determine the effectiveness of those programs without population size estimates.

Density

There is little to no information on python abundance across southern Florida. Abundance is typically estimated using capture-mark-recapture studies of individuals, but because individual detection rates in pythons are extremely low, encounter rates are extremely low and re-encounter rates are even lower, making the cost and duration of this kind of study of pythons an obstacle (see Detection Probability section). Agricultural activities have allowed for rough density estimation at Frog Pond WMA on the eastern edge of ENP (505 ha total area, Fig. 1), where dead pythons were recorded each year after mowing or disc-harrowing operations (22 in 2005, 44 in 2006, 55 in 2007, and 44 in 2008; Reed et al. 2011). During 2009; Reed et al. (2011) found 7 of 11 (>60%) pythons survived Frog Pond WMA agricultural operations and applied this high apparent survival rate to the 2005–2008 data from Frog Pond WMA, yielding estimated densities of 6.9 to 17.1 per km^2. This range is comparable to the estimate of 13.6 per km^2 derived from harrowing activities on 81 ha in 2009. Notably, these are minimum simple density estimates where disc harrowing occurred over several days. Some pythons may have left the study site in response to mechanical disturbance or may not have been detected if buried by disc harrowing. These densities are higher than estimated inside of ENP (< 5 per km^2 between 2003 and 2017; Willson and Pittman 2017) but may be driven by abundant rodent prey typical of fallow agricultural fields (Reed et al. 2011). The Frog Pond WMA was formerly agricultural lands and is bordered by ENP's vast wildlands, whereas Willson and Pittman (2017) discourage using their models in areas such as agricultural or residential, where roadside habitat differs from surrounding habitats.

The only attempt to rigorously estimate python density in southern Florida is a novel, simulation-based technique developed by Willson and Pittman (2017) that does not rely on CMR to estimate density of secretive snakes. Instead, the authors used radiotelemetry data from 13 pythons to parameterize individual-based movement models to estimate the frequency the individual snakes cross roads; they also incorporated 14 years of effort-corrected road surveys (125 python captures), along with survey-vehicle and snake-crossing speeds for 31 pythons, to determine the probability of detecting a snake, given that it crosses the road during a survey. Working under the assumption of no behavioral response (attraction or avoidance) to the road and using average values for road crossing speed, snake crossing time, individual road crossing speed, and encounter rate during road surveys, Willson and Pittman (2017) estimated that Burmese python density in the vicinity of Main Park Road in ENP varied from approximately 1.5 to 5 per km² between 2003 and 2017. This region (Long Pine Key to Flamingo, Fig. 1) contains habitats broadly representative of ENP, including extensive freshwater and brackish marsh, mangrove forests, and pockets of hardwood hammock and pine rockland. If these estimated densities along the Main Park Road are representative of ENP, then extrapolating to the extent of ENP (3,988 km² of non-open water habitat) suggests an approximate population size of 8,000 pythons within the park during 2017 and as many as 20,000 at peak abundance from 2009–2016 (Willson and Pittman 2017). Extrapolations beyond ENP are complicated by differences in habitat and variation in density related to the progression of the invasion outside of ENP, but based on the density estimate for ENP, there may be tens of thousands of pythons across known areas of invasion in southern Florida (Willson and Pittman 2017).

Several factors may have biased Willson and Pittman's (2017) estimate of density, particularly the removal of pythons from Main Park Road for many years (~ 600 removed between 2002 and 2014; Falk et al. 2016, see Visual and Road Surveys section). Therefore, relative to the overall landscape in ENP, the python population around the Main Park Road may be reduced, and these removals may lower road encounter frequency (Willson and Pittman 2017). In addition, assessment of python movement patterns may have been influenced by more extensive movement of adult telemetered pythons compared to juveniles (see Dispersal and Movement sections), which results in overestimated movement rates of adults (Willson and Pittman 2017). Both these factors ultimately would lead to underestimates of python density (Willson and Pittman 2017).

Density estimates of 1.5 to 5 pythons per km² in ENP may be low, especially considering that large, native snake species often exist at densities greater than one per ha (100 per km²; Parker and Plummer 1987). The estimate of 1.5 to 5 Burmese pythons per km² in ENP (Willson and Pittman 2017) is similar to what has been reported for Indian pythons from the native range in India, where Bhupathy and Vijayan (1989) recorded a maximum of 144 and 111 individual pythons over two winters within a 29 km² wildlife refuge, producing an approximate density of 5 per km². However, this estimate may have been biased by double-counting of individuals that switched dens and low detectability of some individuals, especially juveniles (Bhupathy and Vijayan 1989).

Overall, there is little information about python population size within ENP, and no information regarding abundance across southern Florida. The standard technique for robust abundance estimation while accounting for imperfect detection of all individuals in the population is capture-mark-recapture (e.g., Pollock 1976; Otis et al. 1978), and this technique has been reviewed (Seber 1986; Pollock et al. 1990; Schwarz and Seber 1999) and expanded (e.g., Schaub and Abadi 2011; Kendall et al. 2013; Royle et al. 2018). Currently, the most promising way to obtain Burmese python abundance estimates in future studies may be to conduct mark-recapture studies, incorporating many individuals, using radiotelemetry across several study areas representative of the variety of habitats in southern Florida. Abundance estimation and understanding detection are fundamentally linked (see Detection section), and assessment of control effort success will be challenging without the ability to monitor resulting shifts in abundance. However, if robust population estimation is feasible, simpler and less-expensive methods such as an index of abundance could be evaluated (and calibrated) to track changes in abundance over time, or variation in abundance across study areas (e.g., Engeman 2005; Janousek et al. 2019; Bauder et al. 2021; see Future Research section). In addition, further development and validation of novel methods that do not rely on capture-mark-recapture, such as the individual-based model simulations of Willson and Pittman (2017), along with novel population estimation techniques such as removal models, and genetic sampling to infer population demographics, may be promising for estimating python abundance (see Future Directions section) and are in the early stages of evaluation for this species. Further, monitoring prey response to python control efforts may be an alternative or supplemental means to evaluate management actions if the goal is to reduce the negative impacts to the ecosystem rather than to achieve a certain python density on the landscape.

Geographic distribution

The most common method for determining distribution of any species is to plot occurrence records. In the case of Burmese pythons, this approach can depict the spatial spread of snakes over time (Fig. 6) with the caveat that search effort is rarely consistent in all areas over time, which can influence interpretation. There are two other distinct lines of research into the geographic distribution of Burmese pythons. The first aims to delineate the python distribution at any given point in time using occupancy estimation (see Detection section) to infer presence or absence where there have not been sightings. The second is focused on predicting the potential invasive range of Burmese pythons in North America, based on climate matching between their native range and the Americas.

Range in Florida

Determining the python distribution is an ongoing research priority but is challenging because the invasion front is shifting over space and time, much of the landscape is inaccessible, survey effort is not available for many records, and python detection prob-

ability is extremely low (see Detection section). However, there is a large geospatial database of invasive species reports, Early Detection & Distribution Mapping System (EDDMapS; https://www.eddmaps.org), that includes Burmese python observations submitted by python researchers, land managers, and the public. Though distribution records are biased towards accessible areas (levees and roads; Fig. 6), they are useful for determining the extent of the invasive population in Florida. However, there is considerable noise in these data (e.g., data errors, duplicate entries, unconfirmed sightings submitted by the public, and possible snakes of recent captive origin) which cannot be easily separated from valid sightings of pythons from the wild population.

Based on available records, Burmese pythons occupy most of southern Florida, encompassing approximately 30,000 km^2 from Lake Okeechobee throughout Palm Beach County, south through Miami-Dade County to Key Largo, and west throughout Monroe, Collier, Hendry, and Lee Counties (Fig. 6, see History of the Invasive Florida Population section). Burmese pythons appear to be ubiquitous in many terrestrial habitats within ENP (Snow et al. 2007a; Hart et al. 2015; Bonneau et al. 2016; Falk et al. 2016; Smith et al. 2016; Fig. 6). Along the invasion front, where there are few records, northward expansion has been evaluated using eDNA.

Early detection using eDNA

By 2013, the most northern samples documenting Burmese python eDNA were taken south of Lake Okeechobee in Holey Land Wildlife Management Area and the adjacent Stormwater Treatment Area (STA) 5 (Fig. 1, Hunter et al. 2015). To further examine potential northward expansion of the Burmese python population in southern Florida, Hunter et al. (2019) tested water for python eDNA within LNWR, in WCA 1, where pythons had not been previously sighted (Fig. 1, Table 1) in Palm Beach County on the eastern side of the Florida peninsula. The LNWR is one of the last remaining wetlands of the northern Everglades (Jordan et al. 1997). The authors also surveyed adjacent areas to the south (e.g., WCA 3; Bonneau et al. 2016), which had several python records by 2014 (EDDMapS 2018). From 2014 to October 2016, Hunter et al. (2019) collected water samples from 87 sites within LNWR, STA 3/4 to the southwest of LNWR, and WCA 2 and 3 to the south/southwest (Fig. 1, Table 1) and consistently documented the presence of Burmese python eDNA throughout space and time (Hunter et al. 2019). Yet, almost all of these detections pre-dated the first confirmed sighting in the LNWR boundary, which occurred in September 2016 (EDDMapS 2018; Hunter et al. 2019). While most live captures of Burmese pythons are south of the LNWR, eDNA detections indicate a northern range limit at, or north of, LNWR (Hunter et al. 2019). Isolated individuals have been found well outside of these areas, but the exact northern extent of the wild Burmese python population in southern Florida is difficult to determine because of the challenges in distinguishing wild Burmese pythons from recently escaped or released captive animals, and as a result of their cryptic nature and low detectability. Pythons will rarely, if ever, be visually observed when their population density is low (see Detection section).

Potential range

To project the potential range of Burmese pythons in the United States, several species distribution models have been produced with the goal of characterizing the climate of their native range in southeast Asia and identifying sites elsewhere in the world that may be climatically similar and therefore at risk of invasion by pythons. These endeavors provoked public controversy (reviewed in Rodda et al. 2011; Engeman et al. 2014) and produced divergent range predictions (Pyron et al. 2008; Rodda et al. 2009, 2011; Jacobson et al. 2012).

Rodda et al. (2009) identified average monthly rainfall and temperature as predictors of prey productivity and python activity and used these data from within the Burmese python native range in Asia to map areas of the United States with a similar climate (i.e., bivariate climate envelope). This approach suggested that much of the southern third of the United States is potentially vulnerable to Burmese python invasion. Another analysis by Pyron et al. (2008) using maximum entropy modeling (i.e., program MaxEnt, Phillips et al. 2006) suggested that only extreme southern Florida was suitable, but reconstruction of this analysis removing erroneous blood python (*Python brongersmai*) datapoints expanded the climate match to include all of Florida (Rodda et al. 2011).

Overall, potential range limits of Burmese pythons are uncertain. Multiple climate matching efforts have reached different conclusions. In addition, there is evidence that evolutionary change has already altered parts of the genome responsible for cold tolerance (see Cold Tolerance section), and there is the potential for behavioral plasticity to enhance cold tolerance by pythons seeking refugia (see Refugia section). Further, climate change is ongoing and may be outpacing previous climate projections (Abatzoglou et al. 2020; Hausfather et al. 2020). Taken together, this evidence suggests we may at least expect that pythons can tolerate climatic conditions farther north than where the population is currently established south of Lake Okeechobee (see Range in Florida section). Finally, climate is not the only determinant of a species' realized distribution, and the extent to which python populations may be restricted or facilitated by factors other than climate (e.g., prey availability, competitors, disease) remains unclear.

Refugia

Species distribution models have overlaid the range of climate conditions from occupied areas of the native range onto the United States; however, pythons may be able to occupy an expanded climate envelope if released from native-range biotic pressures (e.g., prey availability, competition, predation, refugia, and disease) and if available refugia exist. For example, Burmese pythons use gopher tortoise and mammal burrows as refugia (Metzger 2013; Rahman 2013; Bartoszek et al. 2018a; Hengstebeck and Romagosa 2020), thus interactions with other species are likely to be important in determining the habitable range for these snakes. While some Burmese pythons have been known to seek refuge during cold temperatures, others may lack refuge-seeking behaviors (Avery et al. 2010; Dorcas et al. 2011; Mazzotti et al. 2011; see Physiology

section). The mild temperatures within burrows could help pythons overwinter as far north as southwestern Georgia (Hengstebeck 2018) although free-ranging pythons have not been documented that far north. Model simulations indicate that Burmese python body temperatures within a burrow 30 cm below the soil surface in southern Florida can remain unaffected by either air temperature or body size (Stahl et al. 2016). In addition to tortoise burrows, anthropogenic structures such as culverts, canals, and levee banks may provide access to deep underground refuges (Hanslowe et al. 2016; Stahl et al. 2016).

Cold tolerance

Dorcas et al. (2011) released ten wild-captured pythons from ENP into a semi-natural outdoor enclosure in South Carolina, where winters are appreciably cooler than southern Florida. Although all pythons died over the study, which took place from June 2009 through January 2010, most survived extended periods at temperatures below those typical of southern Florida, including brief freeze events, before dying during a historic cold snap. During this same timeframe, although many pythons died in southern Florida during the 2010 cold spell (Mazzotti et al. 2011, see Thermal Biology section), clearly many pythons survived and all extant wild pythons in southern Florida, or their ancestors, survived the 2010 cold spell. Indeed, Stahl et al. (2016) developed a bioenergetics model to calculate body temperature in various-sized pythons using daily weather data for the Everglades and incorporating python thermoregulatory behaviors to predict body temperatures low enough to result in mortality. Results indicate that for at least one month in every year except 2013 (i.e., 2009–2014) pythons experienced body temperatures that would subject them to significant physiological stress, but estimated body temperatures only dropped to lethal levels in December 2010 (i.e., between 5–10 °C; Stahl et al. 2016). Therefore, survival of pythons may have been facilitated by physiological or behavioral traits that were heritable. Indeed, evidence of a genetic bottleneck in the Florida python population was consistent with the 2010 major freeze event (Hunter et al. 2018). Card et al. (2018) sampled Burmese pythons in Florida before and after the freeze event and found evidence for rapid evolution by natural selection in genes associated with cold tolerance.

Movement

Movement ecology is an ecological subdiscipline that connects an animal's movement path with environmental heterogeneity, available resources, motion and navigation capacity, and its internal state (e.g., motivation; Nathan et al. 2008). Understanding python movements can provide knowledge on home range size and habitat preferences, and these patterns can inform management strategies such as when and where surveys should occur. For example, snake movement patterns differ between the sexes during the breeding season with males moving more (e.g., King and Duvall 1990; Whitaker and Shine 2003; Waldron et al. 2006), presumably to enhance reproductive success. Behavioral trait variation among individuals in personality or temperament

(e.g., Sih et al. 2004; Réale et al. 2007) may also affect movement and activity patterns such as foraging and basking, which may cause population-level differences in movements over time. For example, a simulation study (Mutascio et al. 2017) suggested that dispersal can be influenced by the personality of individuals at the leading edge of the population (i.e., bolder snakes dispersed farther; see Dispersal section).

Adult Burmese pythons are capable of long-distance movements of several km (Hart et al. 2015; Bartoszek et al. 2021b) and they have been documented 7 to 25 km offshore in the Gulf of Mexico (Bartoszek et al. 2018c; Hanslowe et al. 2018). Acceleration data obtained from four wild, female Burmese pythons tracked in ENP indicate that long-distance movements may occur during bouts of continuous transiting lasting several hours; one python transited continuously for 58.5 hours and traveled 2.43 km in a single day (Whitney et al. 2021). In studies of radiotracked adult Burmese pythons, maximum movement rates across individuals varied from 0.11 to 2.43 km/day in ENP (Hart et al. 2015) and 0.18 to 1.94 km/day in southwest Florida (western Collier County; Bartoszek et al. 2021b). Mean daily movement rates across individuals varied from 0.04 to 0.18 (Hart et al. 2015) and 0.02 to 0.14 km/day (Bartoszek et al. 2021b). Daily movement rates reported by Hart et al. (2015) and Bartoszek et al. (2021b) are high compared to data from other large constrictors such as carpet pythons (*Morelia spilota imbricata*) reported to move an average of 100–150 m per week (Pearson et al. 2005). Thus far adult pythons in ENP and southwestern Florida exhibit similar movement rates, despite different habitat composition. Specifically, ENP is dominated by cypress swamps, hardwood hammocks, and wet prairies (Hart et al. 2015), whereas the study area in southwestern Florida (western Collier County) contains a mosaic of natural upland and wetland habitat types in addition to an agricultural and urban environment with a network of roads, canals, and drainage ditches.

In southern Florida, an extensive network of canals and levees may facilitate long-distance movement by pythons, and consequently, expansion across the landscape. However, movement in canals may be a risky strategy due to predation by alligators (Mutascio et al. 2017; Pittman and Bartoszek 2021) and presumably other predators in open water, urban, or agricultural environments, such as wading birds. Compared to adults, juvenile Burmese python daily movement is low (see Dispersal section).

Navigation and homing

Navigational ability is the process by which animals decide when and where to move (Nathan et al. 2008) and may influence the invasive potential of species. For example, navigational capacity may allow animals to exploit resources that are widely spaced or seasonally variable, or reduce risk associated with searching unfamiliar or dangerous areas. Pittman et al. (2014) tracked the movements of 12 adult Burmese pythons in ENP, six of which were translocated 21–36 km from their capture locations to areas presumed to be outside of their regular home ranges. Despite this displacement, translocated pythons oriented toward their capture location, and five of six pythons returned to within 5 km of their original capture locations, demonstrating that Burmese pythons are capable of homing at a scale previously undocumented for any snake

species and without previous experience in the area (i.e., map sense; Pittman et al. 2014). In addition, pythons displayed oriented movement over relatively long-time scales (94–296 days), demonstrating that pythons can maintain long-term movement goals and high motivation to reach home locations, presumably because philopatry increases knowledge of an area and ultimately the likelihood of finding a suitable breeding habitat and mate, conveying a fitness advantage (e.g., Hendry et al. 2004). We do not yet understand how pythons navigate, but presumably pythons sample local environmental cues that vary predictably in space (e.g., magnetic and olfactory cues; Nams 2006) and use polarized light, celestial, or magnetic cues to orient and maintain their bearing over long distances (e.g., compass sense; Southwood and Avens 2010). The strong navigational and homing capabilities exhibited by pythons are useful for future predictions of spatial spread of this species but also have implications for the development of control tools. For example, radiotracked pythons used to locate other pythons (i.e., as scout snakes) may not search areas outside their home range successfully, so the effective spatial area of a particular scout python would be limited (see Scout Snake section).

Dispersal

Dispersal is the movement of organisms away from their place of birth (Bullock et al. 2002), and dispersal behavior strongly influences the dynamics of invasion fronts (Holway and Suarez 1999). Dispersing individuals are expected to be the youngest life stages, including hatchlings and subadults (e.g., Johst and Brandl 1999). Burmese pythons have high navigational capacity (see Navigation section), which may increase the incidence of exploratory movements, potentially increasing the survival of dispersers. However, if large-scale navigational capacity increases as pythons become adults, the risks associated with exploratory movements may decrease and therefore the longest distance dispersal events that drive population expansion may happen as adults. Using model simulations based on empirical dispersal data from southern Florida, Mutascio et al. (2017) found that juvenile Burmese pythons likely have behaviorally plastic movement patterns rather than primarily bold or shy patterns, which is notable because individuals with behavioral flexibility may have better responses to novel conditions (Sih et al. 2012). Along the shy-bold continuum, bolder simulated pythons had higher rates of mortality but also exhibited greater dispersal distances (Mutascio et al. 2017). Increased dispersal of bold snakes combined with sophisticated navigational abilities suggests that personality-dependent dispersal may impact the spread of Burmese pythons at the leading edge of the population. A radiotelemetry study of 28 hatchling Burmese pythons from four clutches tracked for three years found that although survival was lower for clutches deposited near urbanized areas, pythons extensively used canals, exhibiting relatively high net movement rates within these systems (i.e., mean net distance moved after 2 months: urban interface: 569 m (n = 7), forested wetland: 553 m (n = 7), agricultural interface: 2130 m (n = 3), upland pine: 170 m (n = 6); Pittman and Bartoszek 2021). Thus, the population dynamics and spread of Burmese pythons are likely influenced by landscape composition, where

high intensity urbanization may be a dispersal barrier to juveniles, but the presence of extensive canal networks across southern Florida may mitigate some of these negative effects (Pittman and Bartoszek 2021). Although body size of snakes at the agricultural interface was larger at hatching compared to other treatments, and small sample sizes and clutch effects may confound inferences, use of canal networks and other aquatic areas (e.g., coastal waterbodies) by neonate pythons may maximize net movement rates away from a hatch location. Therefore, canals could potentially increase the likelihood of the establishment of satellite Burmese python populations spatially disjunct from the larger source population in southern Florida. More specifically, while movement rates of juveniles (0.005 km/day to 0.045 km/day; Pittman and Bartoszek 2021) are lower than adults (0.02 to 0.18 km/day; Hart et al. 2015; Bartoszek et al. 2021b), movement after hatching is not directed toward an established home range center. Thus, the dispersal movement of juveniles may drive patterns of range expansion even if rates of movement are low relative to adult movement. Additionally, movement rates and propensity to explore novel territory likely vary throughout the first years of life, and more information is therefore needed to identify the life stages most likely to drive population expansion.

Home range

An animal's home range is most commonly defined as the area it uses during the course of normal activities such as foraging and mating but excluding occasional exploratory excursions (Burt 1943). Home range is a rough measure of the sum of behavioral processes encompassed in an animal's normal activities, and the resources required to sustain them. There are a wide range of methods available to estimate the size and position of home ranges from individual tracking data (Kie et al. 2010), including the minimum convex polygon (MCP), a simple metric that draws the smallest polygon around points with all interior angles less than 180 degrees (Blair 1940). Hart et al. (2015) radiotracked 19 adult Burmese pythons (15 female, 4 male) within the core area of the ENP population and estimated mean home range to be 22.5 km^2 (SD = 21.3 km^2; range 1.7 to 87.4 km^2; 95% MCP). These home ranges are much larger than those recently reported by Bartoszek et al. (2021b), who radiotracked 25 adult Burmese pythons (16 male, 9 female) in southwestern Florida and estimated a mean annual home range of 5.3 km^2 (SD = 4.4; range 0.9 to 18.3 km^2; 95% MCP). In Bartoszek et al. (2021b), male pythons had larger mean home ranges (6.75 km^2, SD = 4.83; 95% MCP) than females (2.82 km^2, SD = 1.72; 95% MCP), presumably driven by mate-seeking behavior of males. Smaller home ranges in southwestern Florida may indicate that resource availability for pythons is greater compared to ENP. More specifically, the mammal community is more intact in southwestern Florida than in ENP (Sovie et al. 2016; Reichert et al. 2017), which is heavily impacted by Burmese pythons (Dorcas et al. 2012). Overall, however, any summary of home range can be considered an approximation because resources and habitat shift over space and time, and there is a high degree of individual variation in behavior (Powell and Mitchell 2012). As a result, Burmese python home ranges presumably shift over time subject to available resources.

Habitat use

Aside from potentially differing prey availability, the varying habitats in Florida may also influence movement and home range of pythons. For example, although both ENP and southwestern Florida contain extensive wetland habitats, within southwestern Florida these wetlands are interspersed throughout xeric, upland habitat types that are more predominant than within the "river of grass" ridge and slough system that characterizes ENP (Lodge 2010). Compared to upland areas, extensive wetland habitats may have lower barriers to movement and thus potentially lower energetic costs which may result in larger areas of activity. Although Burmese pythons have been found in nearly all habitat types in southern Florida including freshwater and estuarine wetlands (Mutascio et al. 2018), habitat selection is primarily driven by elevation (Hart et al. 2015; Walters et al. 2016; Bartoszek et al. 2021b). Elevation is low in southern Florida, with many areas near sea level (Weiss et al. 2011), particularly the mangroves within ENP where topography fluctuates by less than 2 m (Simard et al. 2006). Low elevation underscores the importance of upland areas that remain relatively dry, particularly during the breeding or nesting seasons when pythons select higher elevations (Hart et al. 2015; Smith et al. 2016; Walters et al. 2016; Bartoszek et al. 2021b).

Another potentially important factor that may influence home range in southern Florida is urban landcover, which is permeated by an extensive network of canals and drainage ditches that facilitate movement by pythons (Mutascio et al. 2017, 2018; Bartoszek et al. 2021b; Pittman and Bartoszek 2021). Whereas Bartoszek et al. (2021b) found that adult pythons selected freshwater wetland habitats but avoided open water, hatchling pythons in Pittman and Bartoszek (2021) used canals frequently. Different use of relatively open water areas may reflect differences between hatchlings dispersing and adults moving within a home range, or differences in the spatial and temporal scale and distribution of habitat between the two studies. Further, whether the open water of canals or the linear structure of refugia adjacent to the canals facilitated net movements of hatchlings is unknown. Hatchlings using canal systems had access to both open water in canals as well as upland areas adjacent to the canals (Pittman and Bartoszek 2021). Likewise, home ranges may be influenced by refugia within upland sand dune ridges and xeric scrub habitat (e.g., armadillo and tortoise burrows, tree root cavities), and these resources are prevalent in some parts of Florida (e.g., southwest Florida), but less so in others (e.g., ENP). Burmese pythons are known to use gopher tortoise burrows where present (Metzger 2013; Hengstebeck and Romagosa 2020), including during breeding aggregations where as many as 7 adult pythons have been documented within the same burrow, along with a resident tortoise (Bartoszek et al. 2018a). In contrast, large areas of the Greater Everglades are characterized by perennially high water tables, thin peat layers with marl lying close to bedrock, extensive peat subsidence, and numerous holes in the underlying karst limestone bedrock which remain flooded (Lodge 2010). During cold temperatures, dry refugia in the sloughs of the Everglades tend to be limited to uprooted trees and dense clumps of grass and few tree islands with slight elevation (Lodge 2010; Mazzotti et al. 2011), though deep waters also provide refuge from cold temperatures (Hallac et al. 2010) and may be used

for thermoregulation by pythons. The data collected thus far suggest that pythons may differentially use (and move differently) in various habitat types, but because they are using most of the habitats available, habitat type may not be strongly limiting to their current or potential distribution in Florida.

Most research on habitat selection has been at the larger scales of home range and use of habitat types within, but factors characterizing nest site selection in Florida beyond drier elevated habitats are poorly understood. Several single observations have been described in which females selected highly modified habitats such as debris piles (Snow et al. 2007b) or manmade structures along levees or in culverts (Snow et al. 2010; Hanslowe et al. 2016), as well as natural habitats at the base of trees, in tree canopies, in their root systems, or in sandy substrates (Dorcas et al. 2011; Bartoszek et al. 2021b; Currylow et al. 2022a). A detailed understanding of large-scale and microhabitat use by Burmese pythons remains an important knowledge gap to better understand their effects on the ecosystem.

Burmese python impacts

Human safety

There are no reports of humans being killed by wild Burmese pythons in Florida; instead, the few recorded deaths have occurred from captive pythons. People have been bitten by wild juvenile and adult Burmese pythons in Florida, but these events are typically provoked during capture attempts (Reed and Snow 2014), which are more common now that there are several active python removal programs operating in the state (see Removal Programs section) and ongoing python research by biologists. For example, an assessment of incidents in ENP from 2003–2012 reported 5 occurrences of unprovoked Burmese python strikes on humans, all of which were biologists working in undeveloped, inundated wetlands, and none resulted in constriction or serious injury (Reed and Snow 2014). These strikes may have been due to mistaken identity, whereby the pythons struck at what they determined to be potential prey but aborted their actions before constricting or attempting ingestion (Reed and Snow 2014). Such events will likely continue to occur in other locations if pythons expand their range (see Geographic Distribution section) and as research and management efforts continue. Thus far, no unprovoked strikes have been reported towards visitors in ENP despite more than a million visitors per year (Reed and Snow 2014).

Overall, there appears to be very low risk of unprovoked, serious human injury or fatality by wild Burmese pythons in southern Florida (Reed and Rodda 2009; Reed and Snow 2014). Worldwide, we are aware of only one credible report of a human being killed by a wild Burmese python, an infant in Hong Kong in 1900 (Wall 1921; Reed and Snow 2014). Although wild Burmese pythons do pose some risk to humans, particularly from traffic accidents involving large pythons crossing roads (Snow et al. 2007a), the best way to reduce this risk is to avoid interacting with them. Areas near the edges of waterbodies and in dense vegetation in southern Florida may pose higher

risks for human-python conflicts, especially for children, which can be reduced by taking precautions when walking near such areas due to the additional risk of human-alligator conflict (Snow et al. 2007a; Reed and Rodda 2009).

While there is little risk of python-induced injury to humans, there may be some threat from consumption of python flesh. Mercury concentrations are high in tissues of pythons collected from southeast Florida (mean 4.35 mg/kg, n = 136; Rumbold and Bartoszek 2019), where the slowly moving, shallow water marshes of the Everglades are conducive to methylation of atmospherically deposited mercury that bioaccumulates in living organisms (Gilmour et al. 1998; Orem et al. 2011; Rumbold and Bartoszek 2019). In contrast, pythons from southwest Florida have lower levels of mercury in their tissue (mean 0.12 ± 0.19, maximum 1.33 mg/kg THg, n = 123; Rumbold and Bartoszek 2019). Generally, mercury concentrations in southeastern Florida are greater than recommended guidelines indicating no more than 1 mg/kg (i.e., 1 ppm) of mercury be consumed (ATSDR 1999).

Although direct risks to humans may be minimal, python-induced changes to mammal community composition (Reichert et al. 2017; Soto-Shoender et al. 2020) may indirectly increase the risk of transmission of Everglades virus to humans (Burkett-Cadena et al. 2021; see Parasites and Pathogens section).

Direct ecological impacts on wildlife

Burmese pythons consume a wide range of vertebrate prey, particularly mammals, and directly influence and alter food webs throughout southern Florida. Invasive species, particularly invasive mammalian predators, have contributed to extensive global species declines and extinctions (Doherty et al. 2016). Therefore, understanding the impact of Burmese pythons on native prey communities, and possibly mitigating these impacts, can help inform efforts to minimize biodiversity loss across the Greater Everglades Ecosystem.

Foraging strategy

Burmese pythons are considered ambush predators that eat infrequently but consume a wide variety of terrestrial vertebrate prey (Reed and Rodda 2009; see Diet section). Ambush predators are thought to primarily use odor cues to identify trails left by prey species and then conceal themselves near prey pathways, striking when prey approach (Reed and Rodda 2009). In addition to using odor cues, pythons may also use visual and thermal cues supplied by the infrared-sensitive pits on their rostral and labial scales to detect approaching prey (Goris et al. 2007; Grace and Matushita 2007).

Despite the general acceptance that pythons are ambush predators, there are few observations in the wild of this behavior. Whitney et al. (2021) obtained continuous acceleration (i.e., activity, behavior, and energy expenditure) and temperature data from four wild female Burmese pythons in ENP over periods of 19 to 95 days (mean 54 ± 33 days) between September and April and found that pythons spent an average of 86.1% of their time resting. Although resting periods were interrupted by changes

in body position and short movements lasting a few seconds to minutes, pythons typically went for over a day at a time and sometimes several days between transiting events (Whitney et al. 2021). While Burmese pythons are capable of long-distance movements up to several kilometers (see Movement section), the resting periods documented by Whitney et al. (2021) are consistent with many ambush-foraging snakes (Pope 1961; Daniel 2002). However, data from Whitney et al. (2021) are limited to female pythons during the breeding season, a time when females may move less than males (see Movement section). Further, recent evidence of pythons consuming nestlings, fledglings, and eggs of wading birds (via climbing up to 1.5 m) indicate that pythons will actively search for prey (Orzechowski et al. 2019b). The extent to which active foraging by pythons occurs across the population is unknown; however, snake foraging strategies can fall along a continuum of ambush to active strategies (Beaupré and Montgomery 2007). Burmese pythons, a highly mobile species (see Movement section), engage in both strategies, as has been documented in other pythons (Bruton 2013). Overall, little is known about wild Burmese python foraging behaviors, feeding frequency, or growth rates (Josimovich et al. 2021; see Growth and Longevity section). Therefore, understanding the behavioral interactions between pythons and their prey may be critical for understanding, predicting, and mitigating python impacts on native species.

Diet

In both their native range and in southern Florida, Burmese pythons are dietary generalists that consume a wide range of vertebrate prey, consisting mostly of mammals and birds, although there are a few records of lizards, frogs, and snakes from the native range (Wall 1921; Snow et al. 2007c; Reed and Rodda 2009; Dove et al. 2011; Boback et al. 2016; Romagosa et al. 2022). Special attention has been paid to the largest prey taken from python gastrointestinal tracts in both the native range (e.g., leopards, antelope, deer, jackals, porcupine, goats, wild boar, pea fowl, langur monkeys; reviewed in Reed and Rodda 2009) as well as in southern Florida (e.g., American alligators, white-tailed deer [*Odocoileus virginianus*], wild pigs, bobcat, great blue herons [*Ardea herodias*], and federally threatened wood storks [*Mycteria americana*]; Snow et al. 2007c; Rochford et al. 2010b; Dove et al. 2011; Boback et al. 2016; Bartoszek et al. 2018b; Romagosa et al. 2022). However, small prey including cotton mice (*Peromyscus gossypinus*), cotton rats, marsh rabbits (*Sylvilagus palustris*), house wrens (*Troglodytes aedon*), and shrews have been consumed in Florida (Snow et al. 2007c; McCleery et al. 2015; Table 3).

Several methods have been used to identify prey from within Burmese python gastrointestinal tracts including morphological, molecular, and isotopic techniques. Thus far, morphological methods including microscopy have been the most successful for individual prey identification (Snow et al. 2007c; Dove et al. 2011). Feather and hair identification can be challenging and requires microscopic comparison to museum specimens of plumulaceous (downy) barbs on feathers or the medulla and scale pattern of hairs (Dove et al. 2011). Because morphological identification of prey can be challenging, particularly for prey in the hindgut or for young prey that do not yet have adult feathers or hair, molecular approaches to extract usable DNA from python gastro-

intestinal contents have been employed, but with limited success (Falk and Reed 2015). Prey DNA in python digesta was too degraded to be useful (Falk and Reed 2015), likely as a result of efficient digestion and prolonged digestive times up to several months (Lillywhite et al. 2002). Technological advances may eventually make a molecular approach more successful, but labor-intensive morphological approaches are currently the most efficient (Falk and Reed 2015). Stable isotope analysis can potentially reveal the contributions of prey items to a predator's diet, but this typically only works when the number of potential prey items are few, (i.e., typically 2 or 3). Stable isotope analysis has also been used to measure the isotopic niche, a two-dimensional space composed of carbon and nitrogen isotopic values that is closely related to the Hutchinsonian ecological niche in that it measures aspects of both niche space and diet (Newsome et al. 2007). Smith (2016) found that the Burmese python isotopic niche is both wide and plastic, independently corroborating previous studies showing broad habitat and dietary requirements. Furthermore, the Burmese python isotopic niche is one of the largest ever documented (96th percentile of published values; Smith et al. 2018).

Since early 2000, several organizations including the United States federal government (U.S. National Park Service, U.S. Geological Survey), state of Florida (Florida Fish and Wildlife Conservation Commission, South Florida Water Management District), universities (University of Florida), and nonprofits (Conservancy of Southwest Florida) have been removing Burmese pythons across southern Florida and conducting necropsies to identify gastrointestinal contents for a direct account of diet in their invaded range. Expanding on prior studies, Romagosa et al. (2022) examined over 2,200 diet samples from 1,716 Burmese pythons collected between 1995–2021 from across southern Florida, south of Lake Okeechobee, with many records from ENP (57% of samples). Burmese pythons consumed 76 prey taxa, predominantly mammal (n = 26) and bird species or subspecies (n = 48), but also two reptile species (American alligator and green iguana; Table 3, Fig. 8). Thus far, despite their prevalence in southern Florida no fish, skunk, bat, turtle, snake, or amphibian species have been documented in Florida pythons. Small mammals in the order Rodentia (n = 1,157) were the most numerous components of python diet, and of these, hispid cotton rats (n = 528) and black rats (*Rattus rattus*, n =333) comprised 45% of all identified diet items (Table 3, Fig. 8). While rodents were the most common component of python diet, their body size is relatively small and thus larger prey (e.g., deer, boar, alligators) may comprise a large proportion of biomass consumed by Burmese pythons. Other prey species found in python gastrointestinal tracts included round-tailed muskrat (*Neofiber alleni*, n = 94 5.3%), cotton mouse (n = 120, 6.7%), Virginia opossum (n = 77, 4.3%), American alligator (n = 71, 4.0%), and marsh and cottontail rabbits (n = 91, 5.1%; Table 3, Fig. 8). Notably, after rats, round-tailed muskrats were the most prevalent species found in python gastrointestinal tracts (Table 3), yet despite multiple visual surveys between 2007–2009 for a variety of mammals using several methods, round-tailed muskrats were not found by researchers in ENP (Pifer et al. 2009). Thus, pythons may join other snakes such as sea kraits, coral snakes, and garter snakes in their ability to detect (and sometimes newly discover) species that humans have had difficulty documenting (Schmidt 1932; Reed et al. 2002; Séret et al. 2008; Reilly et al. 2010; Campbell et al. 2018).

While mammals were more numerous within python gastrointestinal tracts, birds made up the most diversity. Of the 48 species or subspecies of birds identified in python guts, wading birds (Pelecaniformes, n = 10 species, 20.8%), songbirds (Passeriformes, n = 12 species, 25%), and rails (Rallidae, n = 7 species, 14.6%) comprised most of the bird species diversity (Table 3). American coots (*Fulica americana*, nspaces around = 20 individuals) were the most prevalent species within the rail group, and of wading birds, white ibis (*Eudocimus albus*, n = 44), limpkin (*Aramus guarauna*, n = 21), and American bittern (*Botaurus lentiginosus*, n = 19) were the most prevalent (Table 3, Fig. 8). Songbirds were uncommon prey items (Table 3), likely because compared to other available bird prey, songbirds are less reliant on aquatic areas and less likely to encounter pythons. Although 76 mammal, bird, and reptile taxa have been documented thus far, the list does not likely represent all species pythons are consuming in southern Florida. Indeed, the python prey base may continue to grow as the python population expands to new areas, and despite mammals being consumed in greater numbers, birds may make up most additional species documented over time given high richness of this group (Romagosa et al. 2022).

Species of concern

The presence of large species such as bobcat, deer, as well as a wide variety of highly mobile bird species in python gastrointestinal tracts indicates that almost any native endotherm within southern Florida is vulnerable to predation by pythons. Several species of concern have been documented in python stomachs, including state-threatened species [little blue heron (*Egretta caerulea*), roseate spoonbill (*Platalea ajaja*), Big Cypress fox squirrel (*Sciurus niger avicennia*)], federally threatened species [wood stork], and federally endangered species [Key Largo woodrat (*Neotoma floridana smalli*; Sunquist-Blunden and Montero 2021), Key Largo cotton mouse (*Peromyscus gossypinus allapaticola*)], (Greene et al. 2007; Dove et al. 2011; Romagosa et al. 2022). Other threatened and endangered co-occurring species not yet documented as python prey include the Florida panther, Everglades mink (*Neovison vison evergladensis*), Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*), and American crocodile.

In addition to direct predation, Burmese pythons may compete with native species such as bobcats, Florida panthers, predatory birds, and snakes (e.g., eastern indigo and eastern diamondback) for prey. These native predators also have broad diets and consume a variety of birds, small and mid-sized mammals, and reptiles. In the case of panthers, competition may occur for large mammalian prey such as white-tailed deer and wild hogs (Maehr et al. 1986; Tewes et al. 2002; Caudill et al. 2019).

Ground-dwelling birds such as cranes, coots, and gallinules, as well as wading birds (ibises, storks, spoonbills, egrets, herons) may be particularly at risk because they lack the reproductive output typical of mammals such as rodents or feral hogs, and all life stages (eggs, young, adult) are susceptible to predation by native carnivores, as well as pythons (Dove et al. 2011, 2012). A single Burmese python residing at a wading bird colony may impart significant negative ecological impacts (Smith et al. 2007). However, without data on bird abundance in python-occupied areas, it will be difficult
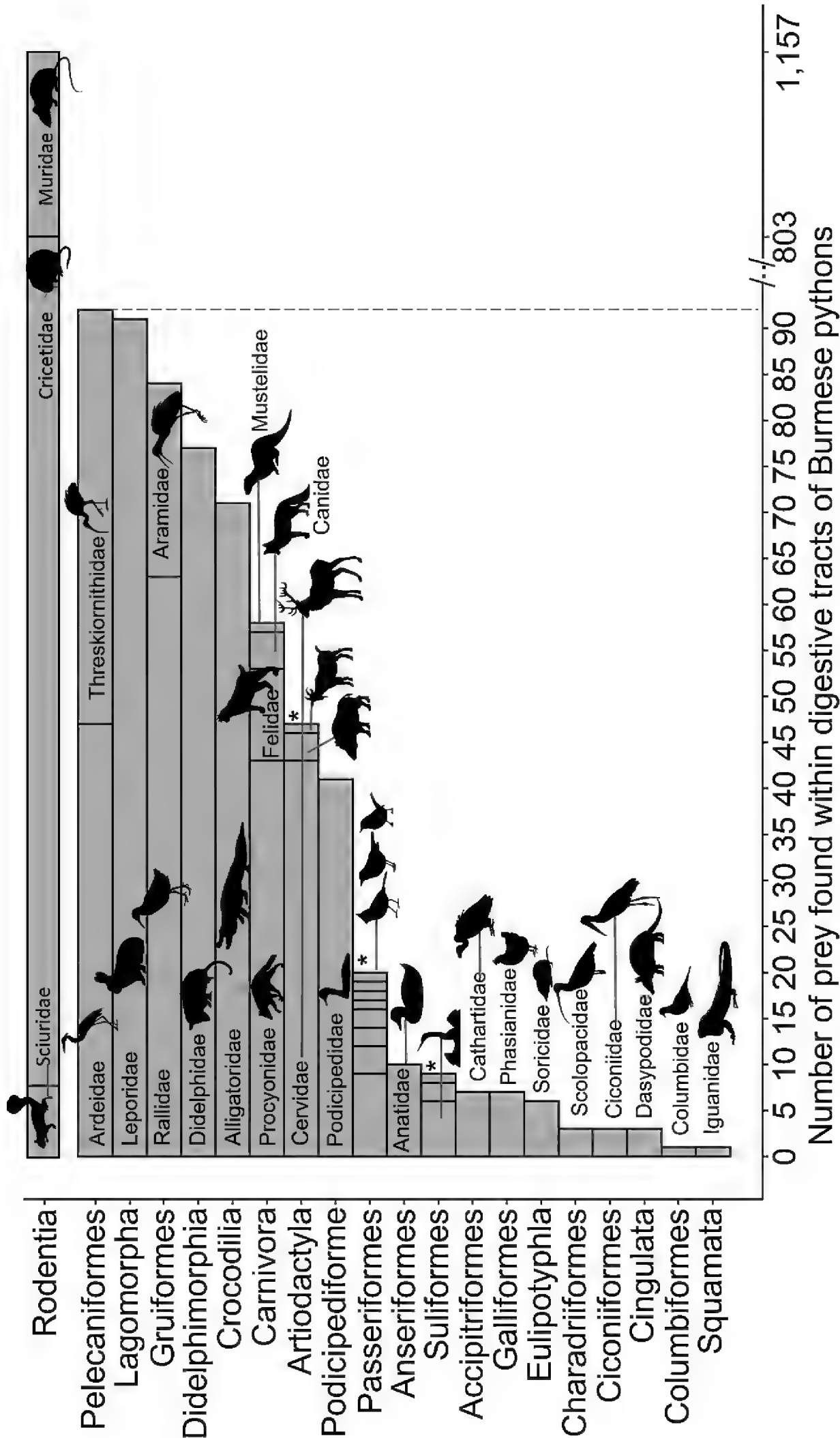
Figure 8. Number of prey by order (y-axis) and family (text within bars) found within stomachs of Burmese pythons (*Python molurus bivittatus*). Black silhouettes are a general representation of animals within each family. Asterisks indicates several unlabeled families including eight within Passeriformes (Icteridae, Troglodytidae, Cardinalidae, Corvidae, Mimidae, Parulidae, Pycnonotidae, Regulidae), three within Suliformes (Anhingidae, Fregatidae, Phalacrocoracidae), and two within Artiodactyla (Suidae, Bovidae). Data from Table 3 and Romagosa et al. (2022).

Table 3. Prey species found within digestive tracts of Burmese pythons (*Python molurus bivittatus*) in southern Florida. Threat status under the United States Endangered Species Act (Gruver and Montero 2018) is indicated where applicable in bold: FE, federally endangered; FT, federally threatened; FT-S/A, federally threatened due to similarity of appearance, ST, state threatened. Reprinted from (Romagosa et al. 2022).

Order	Family	Scientific Name	Common Name	Count
		Aves		
Accipitriformes	Cathartidae	*Coragyps atratus*	Black Vulture	7
Anseriformes	Anatidae	*Aix sponsa*	Wood Duck	2
		Anas acuta	Northern Pintail	1
		Anas crecca	Green-Winged Teal	1
		Anas domesticus	Domestic Mallard	1
		Anas fulvigula	Mottled Duck	1
		Anas platyrhynchos	Mallard	2
		Spatula discors	Blue-Winged Teal	2
Charadriiformes	Scolopacidae	*Gallinago delicata*	Wilson's Snipe	2
		Numenius phaeopus	Whimbrel	1
Ciconiiformes	Ciconiidae	***Mycteria americana (FT)***	**Wood Stork**	3
Columbiformes	Columbidae	*Zenaida macroura*	Mourning Dove	1
Galliformes	Phasianidae	*Gallus gallus*	Chicken	5
		Numida meleagris domesticus	Guineafowl	2
Gruiformes	Aramidae	*Aramus guarauna*	Limpkin	21
	Rallidae	*Fulica americana*	American Coot	20
		Gallinula galeata	Common Gallinule	11
		Porphyrio martinica	Purple Gallinule	4
		Porzana carolina	Sora	8
		Rallus elegans	King Rail	17
		Rallus limicola	Virginia Rail	1
		Rallus longirostris	Clapper Rail	2
Passeriformes	Cardinalidae	*Cardinalis cardinalis*	Northern Cardinal	2
	Corvidae	*Corvus brachyrhynchos*	American Crow	1
	Icteridae	*Agelaius phoeniceus*	Red-Winged Blackbird	3
		Dolichonyx oryzivorus	Bobolink	1
		Quiscalus major	Boat-Tailed Grackle	2
		Sturnella magna	Eastern Meadowlark	3
	Mimidae	*Dumetella carolinensis*	Gray Catbird	1
		Mimus polyglottos	Mockingbird	1
	Parulidae	*Geothlypis trichas*	Common Yellowthroat	1
	Pycnonotidae	*Pycnonotus jocosus*	Red-Whiskered Bulbul	1
	Regulidae	*Regulus calendula*	Ruby-Crowned Kinglet	1
	Troglodytidae	*Troglodytes aedon*	House Wren	3
Pelecaniformes	Ardeidae	*Ardea alba*	Great Egret	7
		Ardea herodias	Great Blue Heron	6
		Botaurus lentiginosus	American Bittern	19
		Butorides virescens	Green Heron	4
		Egretta caerulea (ST)	**Little Blue Heron**	2
		Egretta thula	Snowy Egret	2
		Ixobrychus exilis	Least Bittern	3
		Nycticorax nycticorax	Black-Crowned Night-Heron	4
	Threskiornithidae	*Eudocimus albus*	White Ibis	44
		Platalea ajaja (ST)	**Roseate Spoonbill**	1
Podicipediformes	Podicipedidae	*Podilymbus podiceps*	Pied-Billed Grebe	41
Suliformes	Anhingidae	*Anhinga anhinga*	Anhinga	6
	Fregatidae	*Fregata magnificens*	Magnificent Frigatebird	2
Suliformes	Phalacrocoracidae	*Phalacrocorax auritus*	Double-Crested Cormorant	1

Order	Family	Scientific Name	Common Name	Count
		Mammalia		
Artiodactyla	Bovidae	*Capra aegagrus hircus*	Domestic Goat	1
	Cervidae	*Odocoileus virginianus*	White-Tailed Deer	43
	Suidae	*Sus scrofa*	Wild Boar	3
Carnivora	Canidae	*Urocyon cinereoargenteus*	Gray Fox	4
	Felidae	*Felis catus*	Domestic Cat	5
		Lynx rufus	Bobcat	5
	Mustelidae	*Lontra canadensis*	River Otter	1
	Procyonidae	*Procyon lotor*	Raccoon	43
Cingulata	Dasypodidae	*Dasypus novemcinctus*	Nine-Banded Armadillo	3
Didelphimorphia	Didelphidae	*Didelphis virginiana*	Virginia Opossum	77
Eulipotyphla	Soricidae	*Blarina carolinensis*	Southern Short-Tailed Shrew	3
		Cryptotis parva	North American Least Shrew	3
Lagomorpha	Leporidae	*Sylvilagus floridanus*	Eastern Cottontail	39
		Sylvilagus palustris	Marsh Rabbit	52
Rodentia	Cricetidae	*Neofiber alleni*	Round-Tailed Muskrat	94
		Neotoma floridana	Eastern Woodrat	13
		Neotoma floridana smalli (FE)	**Key Largo Woodrat**	**10**
		Oryzomys palustris	Marsh Rice Rat	28
		Peromyscus gossypinus	Cotton Mouse	120
		Peromyscus gossypinus allapaticola (FE)	**Key Largo Cotton Mouse**	3
		Sigmodon hispidus	Hispid Cotton Rat	528
	Muridae	*Mus musculus*	House Mouse	20
		Rattus norvegicus	Brown Rat	1
		Rattus rattus	Black Rat	333
	Sciuridae	*Sciurus carolinensis*	Gray Squirrel	3
		Sciurus niger	Fox Squirrel	4
		Reptilia		
Crocodilia	Alligatoridae	***Alligator mississippiensis (FT-S/A)***	**American Alligator**	71
Squamata	Iguanidae	*Iguana iguana*	Green Iguana	1
Total number of species				**76**
Total number of diet items				**1788**

to determine if pythons may be impacting this group. For example, in the Greater Everglades, an area with extensive hydrological alterations, wading birds are dependent on water levels, which vary depending on season and management actions, and thus strongly influence the availability and density of prey fishes and invertebrates (Gawlik 2002; Frederick et al. 2009; Lantz et al. 2010). As a result, wading bird occurrence and density vary spatiotemporally across the southern Florida landscape each year (Picardi et al. 2020, D'Acunto et al. 2021), complicating inference on bird abundance and rendering it challenging to link pythons to potential declines in wading bird populations.

Mammal declines

Burmese pythons in southern Florida consume a wide range of mammals (Romagosa et al. 2022; see Diet section). Before 2000, mammals, particularly raccoon, Virginia opossum, and white-tailed deer were encountered frequently in ENP during systematic

nocturnal road surveys, and rabbits (*Sylvilagus palustris* and *S. floridanus*) were frequently observed in opportunistic roadkill surveys (Dorcas et al. 2012). However, from 2003–2011, the frequency of mammal observations [raccoons, opossums, bobcats, rabbits, gray foxes, and white-tailed deer] declined by 85–100% (Dorcas et al. 2012). These species were more common in areas where the python invasion was more recent and most abundant in similar habitats outside the python's introduced range. Further, these apparent declines in mammal populations coincided temporally and spatially with the proliferation of pythons in ENP (see History of Invasion section), suggesting that predation by pythons has resulted in dramatic declines in mammals within ENP (Dorcas et al. 2012).

Subsequently, McCleery et al. (2015) directly linked mammal declines to Burmese python predation and demonstrated that pythons compete with native predators. Using a large-scale experimental manipulation of marsh rabbits, once an abundant species in ENP, rabbits were released to sites where pythons were thought to be either present or absent. Marsh rabbits reintroduced in ENP with tracking collars persisted for five months and produced offspring before being extirpated primarily by pythons in the summer, presumably because pythons increased foraging activity with onset of warmer temperatures. Pythons accounted for 77% of rabbit mortalities within 11 months of rabbit translocation to ENP, but at control sites, no rabbits were killed by pythons and 71% of attributable marsh rabbit mortalities were classified as mammal predations (McCleery et al. 2015). Based on subsequent surveys across the Greater Everglades Ecosystem, marsh rabbits have persisted in areas with native predators but not pythons (Sovie et al. 2016). Additional surveys by Taillie et al. (2021) compared changes in mammal occurrence from 2014 to 2019 between the core (i.e., southern Everglades) and recently invaded python fronts at the northern extent of python invasion, including LNWR (Fig. 6). The authors documented declines in occurrence of medium (e.g., marsh rabbits) and large-bodied (e.g., white tailed deer) mammals within the invasion front but also little evidence of resilience among mammals within the invasion core (Taillie et al. 2021). Of 15 species detected, invasive black rats were the only species to increase in occurrence within the invasion core (Taillie et al. 2021).

Threats to the Greater Everglades Ecosystem not only include invasion of non-native species but also alteration of hydrology throughout the system, water quality deterioration (e.g., nutrients, sulfate, mercury, pesticides, heavy metals), agricultural and urban development, altered disturbance regimes, and climate change (Light and Dineen 1994; Mitsch and Hernandez 2013). To address the role of alternative stressors in mammal declines, Sovie et al. (2016) examined the influence of both pythons and several other threats on the distribution of marsh rabbits in ENP. Distance from the epicenter of the python invasion best explained marsh rabbit occurrence in suitable habitat patches, whereas none of the alternative stressors, including habitat quality, water flow, or contamination, could explain the distribution of marsh rabbits (Sovie et al. 2016). More specifically, estimates of the probability of marsh rabbit occurrence ranged from 0 at the python invasion epicenter to nearly 1.0 far (i.e., 150 km) from the invasion epicenter, providing evidence for pythons being the primary driver of marsh rabbit declines in southern Florida (Sovie et al. 2016). In a landscape-scale exploration of how Burmese pythons and alternative stressors may be structuring mammal com-

munities across 113 sites throughout the Greater Everglades Ecosystem, Reichert et al. (2017) determined that of 14 mammal species, all species except coyotes showed a negative response to longer python residence times. The authors concluded that pythons are likely causing a fundamental restructuring of the food web and declines in ecosystem function (Reichert et al. 2017). However, occurrence of habitat-generalist species (i.e., rabbits, raccoons, white-tailed deer, and coyote) increased near urban areas, indicating these areas may buffer the impact of pythons on species loss and community change (Reichert et al. 2017). In urban areas, generalist mammal species may be more resilient to python impacts because of higher rates of survival and fecundity, or mammals may better persist in developed areas where pythons are detected and removed at higher rates (Reichert et al. 2017). Alternatively, resident pythons may avoid urbanized habitats (Bartoszek et al. 2021b). Taken together, these studies provide multiple lines of evidence that: 1) several mammal populations have declined in areas where pythons occur; 2) Burmese pythons are responsible for these declines; and 3) alternative explanations for the declines tested thus far are not consistent with observed patterns.

Indirect ecological impacts

There is considerable research focusing on direct negative impacts of Burmese pythons in southern Florida. However, indirect effects may profoundly affect native ecosystems, including the spread of pathogens (e.g., serpentovirus) and parasites to native species, alteration of host-parasite dynamics (e.g., Miller et al. 2020; Burkett-Cadena et al. 2021), and trophic cascades resulting from the direct suppression of mammal populations in southern Florida (Willson et al. 2011).

Parasites and pathogens

In their native range, Burmese pythons are host to ectoparasites (e.g., ticks, mites), blood parasites (e.g., hemogregarines), protozoan intestinal parasites (e.g., coccidia), metazoan intestinal parasites (e.g., tapeworms, roundworms), and other endoparasites (e.g., pentastomes; Wall 1921; Christoffersen and De Assis 2013; Rajesh et al. 2015).

In southern Florida, several parasite species infect pythons, including native North American snake parasites (e.g., pentastome, *Porocephalus crotali*, Miller et al. 2018); intestinal roundworm, *Physaloptera hispida*, (Spencer et al. 2022) as well as the non-native Asian pentastome (*Rallietiella orientalis*). Parasite infection in a non-native host can create a pathway for parasite spillover to native wildlife and, although undocumented, possible spillback with pythons increasing disease impacts in native species (e.g., Kelly et al. 2009).

About 13% of pythons in Florida are infected with *R. orientalis* (Miller et al. 2020), a species of pentastome lung parasite known to infect pythons and a wide variety of other southeast Asian snakes in the python's native range (Christoffersen and De Assis 2013). This lung parasite now infects native snakes in southern Florida through parasite spillover (Miller et al. 2018). Thus far, at least 14 species of native snakes have been shown to be infected with *R. orientalis*, including species in the genera *Agkistrodon, Masticophis,*

Crotalus, *Drymarchon*, *Lampropeltis*, *Nerodia*, *Pantherophis*, *Sistrurus*, and *Thamnophis*, generally at much higher prevalence than pythons (6–67%, average 41%; Miller et al. 2020, see also Metcalf et al. 2019). Sample sizes of uninfected native snake species (average of 9 individuals examined) were much smaller than for infected native snake species (average of 100 individuals examined; Miller et al. 2020) so apparent lack of infection could be an artefact of sampling. Among the native species infected by *R. orientalis* is the eastern indigo snake, a federally threatened species in Florida (Miller et al. 2020; Sunquist-Blunden and Montero 2021). Observed prevalence and infection intensity of *R. orientalis* is higher among native snakes compared with pythons (Miller et al. 2020) and *R. orientalis* morphology varies among host species indicating a high degree of phenotypic plasticity (Westfall et al. 2019). Indeed, all infected native North American snake species are immunologically naïve to this novel parasite because they did not co-evolve with *R. orientalis*, thus, they are likely susceptible to exacerbated impacts of infection (Miller et al. 2020). Furthermore, the impacts of spillover exceed the geographic range of pythons, as native *R. orientalis*-infected snakes have been documented more than 350 km north of the northernmost infected python (Farrell et al. 2019; Miller et al. 2020; Walden et al. 2020). *R. orientalis* infect widespread and abundant native and non-native intermediate invertebrate, frog, and lizard hosts (Palmisano et al. 2022), and widespread generalist intermediate hosts have facilitated the spread of non-native pentastomes through native snake communities in tropical Australia (Kelehear et al. 2013, 2014).

Given the diverse assemblage of available hosts in North America, *R. orientalis* may expand both to new areas and new host species (Miller et al. 2020). Similarly, although snake fungal disease (SFD), caused by the fungus *Ophidiomyces ophiodiicola* (Lorch et al. 2015) is known to infect many North American snake species, it has been largely undocumented in Burmese pythons or may not be readily detectable on pythons (Glorioso et al. 2020). However, pythons may be reservoir hosts for the fungus and additional research could help to understand their potential to infect native snake species.

In addition to internal parasites, host switching among non-native and native external parasites have been documented in pythons. Ectoparasites on Burmese pythons have been documented in southern Florida, including non-native ticks (*Amblyomma rotundatum* and *A. dissimile*) and two species of chiggers (*Eutrombicula splendens* and *E. cinnabaris*) native to the United States (Corn et al. 2011). Similarly, recent work identified Burmese python DNA in the blood meals of three mosquito species (*Culex erraticus*, *C. pilosus*, and *C. quinquefasciatus*) collected at a northern Florida facility housing pythons in outdoor enclosures, suggesting that when pythons are available hosts, they are fed upon by native mosquitoes (Reeves et al. 2018). Because all three *Culex* mosquitoes are widely distributed across the southeastern Coastal Plain and occur throughout Florida, and the majority of blood-fed *C. erraticus* fed on pythons rather than 10 other hosts, Burmese pythons are likely a host for this mosquito in southern Florida and may be involved in the transmission networks of mosquito-vectored pathogens (Reeves et al. 2018), including Everglades virus (Burkett-Cadena et al. 2021; see Trophic-structure Changes section).

Burmese pythons have been documented carrying a snake-associated virus in the order Nidovirales that causes respiratory disease (i.e., serpentovirus, reviewed by

Parrish et al. 2021). Serpentoviruses, including a python nidovirus, can be a major cause of disease and mortality in captive pythons (Stenglein et al. 2014, O'Dea et al. 2016; Hoon-Hanks et al. 2019). Surveys of wild pythons (n = 172) in southern Florida since 2018 have documented a high prevalence (~24%) and diversity of serpentovirus infection, including geographic segregation among virus variants, with southwestern Florida exhibiting a genetically distinct variant from the rest of southern Florida (Tillis et al. 2022). Other studies have likewise found high prevalence of serpentovirus (50%, n = 52), attributed to timing of sampling, indicating that viral infection may be seasonal (Claunch et al. 2022). No mortality or apparent fitness impacts have been documented in wild Burmese pythons in Florida, and there has been no evidence of spillover from python viruses to native snake species to date (n = 219 snakes across 18 species; Tillis et al. 2022). Yet, native snake sampling for serpentovirus thus far has not fully encompassed the sequence diversity of serpentoviruses occurring in Burmese pythons across southern Florida, and further research on the potential for spillover to native herpetofauna would be valuable (Tillis et al. 2022).

Trophic-structure changes

Brown treesnakes are widely recognized as having caused ecosystem effects on Guam by extirpating or suppressing most of the island's vertebrate species, including important pollinators and seed dispersers, thereby influencing forest diversity (Savidge 1987; Fritts and Rodda 1998; Perry and Morton 1999; Mortensen et al. 2008; Wiewel et al. 2009; Campbell et al. 2012; Rogers et al. 2012, 2017). Additional examples of ecosystem-level impacts of invasive snakes in island ecosystems are emerging, including the horseshoe whip snake (*Hemorrhois hippocrepis*; Montes et al. 2021) on Ibiza and California kingsnake (*Lampropeltis californiae*; Piquet and López-Darias 2021) on Gran Canaria. The Burmese python is the first well-documented example of such impacts in a mainland ecosystem, with a rearrangement and simplification of the mammal community that has begun to alter other ecosystem processes (Reichert et al. 2017; Soto-Shoender et al. 2020; Burkett-Cadena et al. 2021). More specifically, Burmese python predation of native species has caused declines in the occurrence of common mesomammals (Sovie et al. 2016; Reichert et al. 2017). These mammal declines have reshaped the mammal community, with larger, fecund species or those with wide habitat breadths (e.g., black rats, Virginia opossums) being less susceptible to increasing relative densities of pythons, while specialized species with reduced reproductive capacity (e.g., bobcat, Everglades mink) may be more vulnerable (Soto-Shoender et al. 2020). Alternatively, the high fecundity displayed in many rodents can increase their resilience to predation pressures providing a possible mechanism for non-rodent species declines described in Reichert et al. (2017) and Taillie et al. (2021; see Mammal Declines section). As a result, newly created rodent-dominated communities have altered disease dynamics (Burkett-Cadena et al. 2021) and are likely to cause shifts in key ecological processes such as seed dispersal, scavenging, and nutrient cycling. Additionally, the persistence of rodents may result in a stable food source for pythons in areas without other mammal species (Soto-Shoender et al. 2020; Taillie et al. 2021),

as has happened on Guam where invasive brown treesnake populations are sustained by rodents and lizards in the absence of avifauna (Fritts and Rodda 1998).

Declines in mesomammal predators may also indirectly affect other trophic levels, given that many are well-known as predators of reptile nests, particularly turtle nests (e.g., raccoons, opossums, and foxes; Ernst and Lovich 1999). To evaluate indirect effects of pythons on nesting success of egg-laying species, Willson (2017) monitored 183 artificial turtle nests at 13 sites across southern Florida. Turtles are a vital part of many ecosystems, including those of the Everglades, and predation rates on turtle nests can often exceed 90% (Congdon et al. 1986; Ernst and Lovich 1999). In ENP, where pythons have been established the longest and mammal densities were low, corresponding nest predation rates were low. However, at recently invaded sites, nest predation rates were intermediate, and at sites with few or no pythons, predation rates were high (Willson 2017). Low predation pressure by midsized mammals in ENP, where pythons have been established for the longest time, suggests that the direct suppression of mammal populations by Burmese pythons has strong potential to result in indirect effects on non-prey species (Willson 2017). Further, these indirect effects may result in trophic cascades that alter numerous aspects of ecosystem structure and function such as positive effects on other oviparous species, negative effects on other predators via reduction in shared prey (i.e., increased competition), or changes in vegetation dynamics and succession as a result of declines in mammalian herbivores (Willson 2017).

Changes in food web structure or ecosystem services are often intricate and difficult to study and predict, especially in complex food webs where the possibility for compensation or redundancy of species' roles may exist (Pace et al. 1999). Compensatory effects (i.e., a species increases in abundance in response to the reduction of another) and niche exchange because of python predation have not yet been documented but may be likely in a complex ecosystem like the Everglades. For example, Willson (2017) found nest-predation rates by crows were highest in the region where mammals had declined the most, suggesting potential compensation could be occurring, though there may be confounding factors including a lack of historical data on crow prevalence and possibly high crow densities as a result of human subsidization (Willson 2017). It is unclear how the Everglades food web will be able to compensate for loss of roles typically played by mammals. The loss of marsh rabbits and similar species will likely alter trophic interactions and ecosystem function within the Everglades (Sovie et al. 2016), particularly because marsh rabbits likely functioned as a keystone species through their important roles as primary consumers, seed dispersers, and prey for a variety of predators (Blair 1936; Bond 1994; Delibes-Mateos et al. 2008).

Python-induced mammal declines have also indirectly influenced transmission of zoonotic pathogens. Everglades virus is a mosquito-borne (*C. cedecei*) zoonosis of the Venezuelan equine encephalitis complex that is endemic to Florida and causes occasional nonfatal neurological disease in humans (Coffey et al. 2006). The percentage of blood meals taken from the primary reservoir host, the hispid cotton rat, increased dramatically from 1979 (14.7%) to 2016 (76.8%), while blood meals from deer, raccoons, and opossums decreased by 98.2% over the same time period (Hoyer et al. 2017). While raccoon, opossum, and deer have declined in ENP, stable or increasing rodent popula-

tions (Reichert et al. 2017; Soto-Shoender et al. 2020) may create a larger reservoir of Everglades virus, which could increase infection prevalence in mosquitoes, and may indirectly increase the risk of transmission to humans (Burkett-Cadena et al. 2021).

What do we know about control tools?

Management of invasive reptiles is a complex and challenging problem. A wide range of tools and techniques are available to detect and capture snakes (Dorcas and Willson 2009; Dodd 2016), but few techniques are reliable for management of invasive reptiles because many have not been tested to determine biases in detection probability or the degree of population control offered (Dorcas and Willson 2009; Kraus 2009; Reed and Kraus 2010). Further, development of successful control tools requires large and sustained investments in funding, staff, and equipment, without which there are delays in mitigating the negative impacts from invasive reptiles to ecosystems and economies. More recently, awareness of invasive reptiles has increased as a result of their increasing pace of invasion (Reed and Kraus 2010), but thus far, the brown treesnake is the only snake species for which control tools (i.e., visual searches, traps, toxicants, detector dogs) have been well-developed, scientifically evaluated, and shown to be successful for population control (Rodda et al. 2007; Tyrrell et al. 2009; Christy et al. 2010; Lardner et al. 2013). In contrast, although a wide variety of techniques have been employed to catch Burmese pythons across southern Florida (Table 4), many of these tools have not been evaluated scientifically, and the absence of effective landscape-level tools has prevented initiation of any concerted efforts aimed at suppression or eradication, even in limited areas.

Visual and road surveys

Burmese pythons are rarely seen, and even pythons located in accessible areas (i.e., adjacent to roads and levees) or outfitted with radiotransmitters are very difficult to find because they are usually concealed in vegetation or under water (Reed and Rodda 2009; Dorcas and Willson 2013). The method that currently accounts for most python observations and removals is visual surveys on foot or in vehicles along roads, trails, levees, and canals (Figs 6, 8) because these areas are easily accessible to humans, and pythons are more visible due to reduced cover (see Detection section). Vehicles cover more ground than pedestrian surveys, so most visual surveys are conducted by systematically driving (i.e., road-cruising, Smith et al. 2016) along roads and canal levees looking for pythons that are crossing the road. Surveys typically occur at night except for during winter when diurnal surveys can target adult pythons basking along levees (Falk et al. 2016). Importantly, these accessible areas (primarily roads) represent a small fraction of the area occupied by pythons across southern Florida (Fig. 1). For example, in ENP roads accessible to the public (e.g., Main Park, Royal Palm, Old Ingraham, Research, Long Pine Key, Mahogany Hammock, and Pa-hay-okee Roads) sum to approximately 85 km in length. Incorporating a buffer of 1 km on either side

Table 4. Methods used to detect and capture Burmese pythons (*Python molurus bivittatus*). Abbreviations for the timings of application include year-round (YR), breeding season defined as December through March (BS), and late summer (LS) during the hatchling dispersal window which occurs in August. Abbreviations for life stage targeted include reproductive adult (RA), all size classes (All) and all size classes, but dependent on prey size (All*). The cost estimates may vary according to management area or agency and may change over time.

Methods to locate and/or capture Burmese pythons	Timing of Application	Life Stage Targeted	Primary Use	Key Limitations	Cost Estimate	References
Visual Surveys						
Visual Surveys: road cruising	YR, LS	All	Removal	Most of the landscape is > 1 km from a road and these areas can sustain populations	~$298 per python removed (python contractors)	Mazzotti et al. 2011, Smith et al. 2016; Falk et al. 2016; McCaffrey et al. 2022
Visual Surveys: diurnal pedestrian	BS	All	Removal, particularly reproductive adults	Inefficient and costly because of low individual detection (i.e., <0.05)		Mazzotti et al. 2011, Reed et al. 2011, Nafus et al. 2020
Scent detection dogs	YR	All	Detection, Rapid Response, Range Delimitation	Hot/humid temperatures and dense vegetation limit dog performance	Can be as low as $65-100k/yr; $150-250/km; $730-$1,520/day	Romagosa et al. 2011; FWC 2017
Artificial refugia	YR	All	Detection, Removal	Low yield method to detect pythons		Snow et al. 2010, Hanslowe et al. 2016
Burrow camera	YR	All	Detection	Low yield method to detect pythons		Snow et al. 2010, Hengstebeck and Romagosa 2020
Tracking						
Scout snakes	BS	RA	Removal, particularly breeding females	Labor intensive, expensive	~$11k/python; less expensive with less air support Some programs as low as $1,800/python	Smith et al. 2016
Telemetry (of prey animals)	YR	All*	Detection, Removal	Inefficient, low yield		McCleery et al. 2015
Trapping						
Baited trap (python prey, female python)	YR	All	Detection, Removal; Indirectly survey until trap is sprung	Lack of suitable attractant or traps that pythons will enter	Traps less expensive (<$200/trap); labor and vehicle cost are more expensive	Reed et al. 2011, Gati et al. 2020
Drift fence	YR	All	Detection, guide python into a trap	Height and material to prevent climbing over; thus far pythons do not readily enter traps		
Burrow trap	YR	All	Removal	Requires previous knowledge of python presence in burrow, frequent monitoring		Hengstebeck and Romagosa 2020
Camera traps	YR	All	Detection, Indirect and continuous surveying	Potentially millions of photos can result; automated algorithms cannot yet identify pythons; Does not result in capture		Orzechowski et al. 2019b, Gati et al. 2020
Biological						
eDNA	YR	All	Detection, Range Delimitation	Does not result in capture; DNA can be transported		Piaggio et al. 2014, Hunter et al. 2015, Kucherenko et al. 2018, Orzechowski et al. 2019a

Methods to locate and/or capture Burmese pythons	Timing of Application	Life Stage Targeted	Primary Use	Key Limitations	Cost Estimate	References
Pheromones	BS	RA	Removal	Pheromonal lures have not yet been well-developed or successful		
Mechanical						
Infrared (handheld gun/ drone)	YR	All	Detection, Removal	Infrared technology is still being explored as a tool to increase detections during road cruising		Driggers et al. 2019, Hewitt et al. 2021
Mowing/discing	YR, BS	All	Detection, Removal	Limited to agricultural lands and easements along levees		Reed et al. 2011

of these roads represents an area of 170 km², or 3.3% of the land area of ENP, which is 5098 km² (1007 km² of the 6105 km² total area of ENP is Florida Bay; (Schmidt 1979). Therefore, approximately 97% of the landscape within ENP that is habitable to pythons is more than 1 km from a road.

Removal programs

The SFWMD, FWC, and NPS have implemented python removal programs to pay contractors or authorize trained volunteers to capture and remove pythons across southern Florida (Falk et al. 2016, FWC 2022, SFWMD 2022; Table 1). Removal programs operate across SFWMD and other state lands, as well as United States Department of the Interior lands. More specifically, the FWC and SFWMD python removal programs began in 2017 and contractors work on lands managed by FWC, SFWMD, NPS (BICY, BISC, ENP), USFWS (LNWR) and the Florida Department of Environmental Protection (FDEP; Florida State Parks and RBNERR; Fig. 1, Table 1). Contractors are paid an hourly wage and receive additional payment for removing pythons, with larger pythons bringing larger payments. Volunteers in the NPS program are not paid or otherwise incentivized for their efforts beyond their authorizations to search for pythons on NPS lands (Falk et al. 2016). Both contractors and volunteers typically conduct road-cruising surveys, sometimes from elevated viewing positions on vehicles, equipped with lighting, although other methods are available (e.g., boats, walking), and pythons are removed after they are spotted on roads, road edges, or in shallow water next to levees. As of 31 December 2021, removal programs have eliminated at least 13,746 pythons (Fig. 7; Suppl. material 2). To date, most removals with length recorded (SFWMD, 95% of n = 1,407; FWC, 97% of n = 3,304) are of pythons less than 300 cm SVL, and two-thirds (SFWMD, 69%, n = 969; FWC, 66%, n = 2,269) are less than 200 cm SVL (Suppl. material 2), which is the approximate minimum maturation size in southern Florida (see Size at Maturity section). Because of low individual detection compounded by the vast and largely inaccessible Greater Everglades Ecosystem (see Detection section) there are little to no data on Burmese python vital rates, which currently precludes analyses needed to evaluate the effects of removal on python population dynamics (see Demography section). Therefore, it is unclear whether removals of

predominantly immature pythons are effective for reducing abundance or population growth rate (see Abundance section). Overall, across southern Florida, most Burmese pythons are captured on roads or canal levees (Fig. 6), or in water next to levees, and these snakes, particularly in ENP, are predominately non-reproductive juveniles and small adults (Falk et al. 2016; Smith et al. 2016; SFWMD 2022), although very large individuals over 400 cm are occasionally captured (Fig. 4; Suppl. material 1).

Cost of visual surveys

Over the course of two years from 1 May 2019 to 30 April 2021, FWC contractors (see Removal Programs) conducted 4,731 surveys and removed 2,107 Burmese pythons (McCaffrey et al. 2022). The cost of these surveys was approximately $628,471, which includes FWC staff salaries, contractor wages, and material costs, resulting in a cost of $298 per python and 0.09 pythons per survey hour (McCaffrey et al. 2022). This cost is lower than some other methods (see Scout Snake section); however, during certain parts of the breeding season (e.g., December to March), road-cruising may be less effective than using scout snakes if larger, reproductive individuals are the target.

Future applications of visual surveys

Although visual surveys currently result in the highest number of Burmese python captures (see Removal Programs section), it is unclear whether intensive road removals can act as resource protection (i.e., providing localized suppression to protect road-adjacent prey communities over the long term). While visual surveys are currently the most-used control tool for Burmese pythons, the vast roadless areas across southern Florida offer enough suitable habitat to sustain the python population indefinitely and serve as a source for recolonization of the roadside areas (see Challenges Interpreting Removal Data section). Thus, a combination of visual surveys and several other detection and control methods would likely be necessary to suppress the population of Burmese pythons across the entire occupied range, if it is possible at all. In addition, advances in technology may reduce cost per python removed. For example, human eyesight can detect light with wavelengths from 400 to 700 nanometers (nm; Randhawa et al. 2015), yet Burmese pythons may be more easily detected against southern Florida foliage at 850 nm (Driggers et al. 2019; Hewitt et al. 2021). Drones or vehicles mounted with near-infrared cameras implementing artificial intelligence may increase the number of pythons removed from roads during visual surveys by possibly detecting additional pythons at an 850 nm wavelength that visual searchers may have otherwise overlooked.

Scout snakes

The scout technique uses radiotelemetry to capitalize on social behaviors of animals (e.g., seasonal aggregation) to improve detection and to reduce nuisance or invasive populations (Taylor and Katahira 1988; Bajer et al. 2011). The scout methodology has been applied to a variety of taxa and although initially described as the Judas tech-

nique, recognition of cultural associations between duplicity and that term has resulted in alternative nomenclature (e.g., scout) as a more neutral description of the method (reviewed in Fitzgerald et al. 2021).

Although pythons are not typically social, from December to March in Florida they may form breeding aggregations that have been observed to include up to eight pythons (Smith et al. 2016; Bartoszek et al. 2018a; see Reproduction section). More recently, researchers and managers have capitalized on this breeding behavior and used radiotelemetry to track radiotagged scout snakes that reveal the location of other pythons during the breeding season, thereby allowing removal of additional snakes from the population (Smith et al. 2016).

To evaluate the scout snake technique, Smith et al. (2016) radiotracked 25 adult Burmese pythons during the breeding season in ENP, documenting eight scout-associated aggregation events that resulted in capture of 14 new individuals. Bartoszek et al. (2021b) radiotracked 45 adult Burmese pythons in southwestern Florida and located 108 new individuals (55 females, 53 males). Whereas road surveys generally detect smaller, non-reproductive Burmese pythons and are cheaper per python removed (see Visual and Road Surveys section), the scout snake technique yields large, reproductive female pythons (Smith et al. 2016; Bartoszek et al. 2021b). Because the scout snake technique uses mate-seeking behavior of adult pythons to reveal breeding pairs or aggregations, the average size of female pythons found per scout-associated capture event (428 cm SVL, n = 8, SD = 47; Smith et al. 2016) is much larger (i.e., more reproductive potential) than the average size for females caught during road cruising (170 cm SVL, SD = 88, n = 2,377; Suppl. material 1) or incidental captures (262 cm, n = 154, SD = 57; Smith et al. 2016). The published record number of eggs in a wild Florida python (87 eggs) came from a female associated with a radiotagged male scout snake (Krysko et al. 2012), underscoring the impact that removal of these pythons may have on populations.

In areas where multiple control tools are deployed simultaneously (see Removal Programs section), there is a risk of accidental removal of scout snakes, but this can be mitigated by external markers and effective communication. Thus far, the primary method used to externally mark scout pythons in southern Florida is with brightly colored polyolefin tubing (T-bar style Floy tags) shrink-wrapped around monofilament tags and anchored subcutaneously (e.g., Eversole et al. 2014). Contractors that capture scout snakes are required to photograph the tag, report the python, and release the scout at the site of capture, and verified reports result in additional payment. Thus far, four externally marked pythons have been reported to researchers, but only two were photographed and released alive (M. Spencer, FWC, Written Communication, 05/05/2022). There are ongoing efforts to increase awareness of research pythons to members of the public.

Cost of scout snakes

Using data from five seasons of scout snake radiotelemetry efforts, Smith et al. (2016) estimated total cost for an average scout snake field season to be approximately $30,880, which includes the 2015 labor rate of two field technicians in southern Flor-

ida ($5,915), fixed-wing telemetry ($8,403), helicopter flights ($13,906), vehicle fuel ($2,350), and refurbished radiotransmitters ($306). In this study, using scout snakes cost approximately $11,029 per python removed (0.32 pythons per 100 person-hours, average of 2.8 new pythons per season). However, other scout programs also focused on collecting demography data in a relatively large area away from roads and estimated approximately $5,000–7,000 per python removed, which includes a biologist salary to manage the program, flight time for year-round python monitoring, volunteer housing costs, and equipment maintenance (M. McCollister, NPS, Written Communication, 12/27/2021). Finally, the estimated cost of scout programs focused on maximizing removals of reproductive adults (females, n = 171, mean TL = 383 cm, SD = 64; males, n = 146, mean TL = 290 cm, SD = 44) in a relatively accessible and small geographic area (~259 km^2) is approximately $1,800 for each python removed, when averaged across six breeding seasons and accounting for two full time biologists, telemetry flights, and equipment (I. Bartoszek, CSWFL, Written Communication, 4/12/2022).

In general, the costs of using scout snakes are expected to vary widely, depending on location, habitat accessibility, and aviation time and type; programs that do not rely heavily on flight support are likely substantially less expensive per python removed. Personnel in fixed-wing aircraft (i.e., small airplanes) can find the general locations of telemetered snakes and guide technicians on the ground, and helicopters may be necessary to transport staff to and from remote sites where other means of transport are not viable (Smith et al. 2016). Future advances in technology, such as fixed geologging stations or drone monitoring may reduce these costs.

Future applications of scout snakes

Although scout snake programs are more costly per python removed than road cruising, scout snakes are a tool targeting the removal of large, reproductive pythons that are far from roads and that might not be captured otherwise (see Detection section). This technique is implemented during the breeding season when pythons aggregate, and thus scout snake programs may reduce overall costs by increasing tracking frequency during the breeding season and reducing tracking during the remainder of the year. Although both male and female Burmese pythons lead researchers to breeding aggregations and are similarly effective in that they result in similar numbers of pythons removed, programs that use male pythons as scout snakes may lead to the removal of more females (Smith et al. 2016).

Because there may be individual variation in reproductive activity each breeding season among pythons, there is not yet a consensus on what traits make a scout python successful at finding other pythons. Scout success may vary by python density and is complicated by search difficulty in some habitats, but unlike removals by human searchers, the technique is not limited to roads and levees. Ultimately, very high, sustained funding would be required to determine if the scout snake technique can be scaled to a level of effort large enough to impact the population. Important considerations for using scout pythons are their powerful homing and navigational abilities (see

Navigation and Homing section; Pittman et al. 2014). Whether a translocated scout will search an area outside of its home range or immediately try to return home has not yet been evaluated. To increase the efficacy of scout animals, sterilization before deployment in the field has been suggested (Campbell et al. 2005). However, surgical sterilization of male snakes may reduce mate-seeking behavior if circulating hormone levels are appreciably altered, and sterilizing scout males may not constrain python population size or slow its growth if there are no shortage of males in the local population. More specifically, if there are few scouts on the landscape relative to unmarked males, and we assume that sex ratios are equal, females exhibit sperm storage, and multiple males aggregate around single females, then males are not limiting (e.g., Caswell 2001). Additional information about spatial or temporal patterns in hormones and behaviors of scouts leading to associated python captures is needed to make the scout snake technique more efficient. The scout technique will likely remain most cost-effective in areas that are easily accessed by vehicles (e.g., southwest Florida) because it better facilitates radiotracking on foot (e.g., quicker access, reduced bushwhacking) and minimizes some of the need for aerial telemetry support. However, compared to visual or road surveys alone, scout snake surveys result in detection of pythons farther into remote areas and are less biased towards pythons that use human-accessible habitats as part of their home ranges.

Overall, scout program costs do not scale linearly with the number of scout snakes, and there may be opportunities to leverage economies of scale with a larger scout program. While all scout snakes provide important life history data (which are currently limited; see Demography section), the criteria that define a productive scout snake vary according to program objectives. Some scout snakes may make large movements in and out of focal areas, rendering them more difficult to consistently track, whereas others may less consistently locate other pythons; in both cases those scouts increase program costs. Similarly, male scouts may locate females that a research program may opt to leave in the wild and track to obtain demography data; in these cases, male scouts may stay with that female, thus reducing opportunities to locate additional pythons for removal. Where management is the primary goal and in cases where particular scouts appear to be underperforming, it may be necessary to eliminate them to increase efficiency of removals.

Trapping

Using traps to catch snakes circumvents the need for an observer to locate individuals, reducing bias and making it possible to survey difficult habitats during all hours or until a trap is sprung. For decades, snakes have been successfully captured by traps equipped with funnel-style entrances (Imler 1945; Fitch 1951), and modified versions have been developed for use in aquatic, terrestrial, and arboreal habitats (Rodda et al. 1999; Willson and Gibbons 2010; Willson 2016). Funnel traps may contain bait or some other form of attractant, and they can be used in isolation or placed alongside natural or artificial barriers (i.e., drift fences) that act to intercept and guide snakes

into traps (Burgdorf et al. 2005; Fitzgerald 2012). Whereas funnel traps use a narrow opening to guide animals, other traps have entrances that completely close upon entry (Rodda et al. 1999). For example, a modified Tomahawk trap (i.e., Tomahawk model 643 or large reptile trap) has been developed to target large reptiles yet exclude non-target species by incorporating two spring loaded trip pans which must be simultaneously depressed to close the trap (Humphrey 2013; Gati et al. 2020). The trap can only be triggered by an animal long and heavy enough to depress both trip pans at once. Traps may also be placed in areas that pythons might use as refuge, such that the refuge itself acts as an attractant. For example, unbaited traps used to catch gopher tortoises (Enge et al. 2012) have been modified to remove Burmese pythons in burrows (Hengstebeck and Romagosa 2020). Traps are placed over the burrow entrance and include a hinged door that can only be pushed open from below, thus trapping pythons as they exit a burrow. As with funnel traps, both the large reptile and burrow traps must be checked daily to ensure safety of non-target species.

Traps deployed in southern Florida that are sized for pythons need to provide avenues for escape or release of non-target species. Among the key non-targets are endangered or threatened species such as Key Largo woodrat and Eastern indigo snake, as well as species typically destructive to traps (e.g., raccoons, alligators, rats), sensitive species (e.g., birds), and venomous snakes because they are dangerous to remove from traps (Reed and Rodda 2009). Thus, traps which are not target-specific, such as the large reptile trap, need to be checked daily to release the non-targets safely and avoid incidental mortality.

Experiments

Funnel trapping

To assess the efficacy of traps for Burmese python population control, Reed et al. (2011) conducted a medium-scale (6,053 trap nights; ~3 ha) experiment using traps baited with live rats in the Frog Pond WMA east of ENP (Fig. 1). This area was known to be occupied by pythons, as between 22 and 55 pythons were removed annually from 2005 through 2008 (i.e., found dead in fields following mowing or disc harrowing) across a large area (505 ha) encompassing the trapping site (Reed et al. 2011). Despite annual removals during 2005–2008, many pythons likely remained given low detection of the species (see Detection section). Traps were arrayed as a grid of 40 traps placed at 33-m intervals along 10 transects cut through the vegetation, with 10-m spacing between transects. Additionally, three other sites were surveyed with up to nine traps placed around small tree islands. Traps measured 183 cm long × 69 cm wide × 51 cm tall, with a frame constructed of untreated lumber, sides and base sheathed in metal hardware cloth, and a plywood top with a large access door. All traps had a one-way entrance at each end made of a plastic entrance funnel or hardware cloth ramp (see Reed et al. 2011 for detailed information on trap design and construction). Despite a relatively high effort (40 traps checked daily August–November 2009), traps captured

only three pythons along with 69 individuals of various rodent, amphibian, and reptile species (Reed et al. 2011). Following the trap trial, a large area (81 ha) encompassing the trapping site was disc-harrowed, revealing eleven more pythons and large numbers of rodents (Reed et al. 2011). Thus, the trap trial captured only a small proportion of the pythons observed in the study area during this time. Relatively few captures may be a result of behavioral (e.g., ambush predation) or environmental (e.g., high prey density in the study area) factors that reduced the likelihood that a python would encounter, be attracted to, and enter a trap (Reed et al. 2011). While snakes may reduce foraging frequency in a prey-rich environment (Gragg et al. 2007; Tyrrell et al. 2009), scent from abundant prey may also mask the scent from food-baited traps, further reducing encounter rates. Alternatively, traps may have been suboptimal in their design or choice of attractant (live laboratory rat), potentially failing to attract pythons or frustrating their efforts to enter (Reed et al. 2011).

Large reptile traps

Preliminary trials in outdoor enclosures examined effectiveness of the large reptile trap (i.e., a Tomahawk model 463) with three large native snakes (2 cottonmouths and 1 yellow rat snake, *Pantherophis alleghaniensis*); results were promising, as native snakes did not trigger the traps to close, but pythons did (Avery et al. 2014). Gati et al. (2020) performed field trials during 2019–2020 at both the L-37 and LNWR which indicated large reptile traps are effective at nearly eliminating non-target species captures (two non-target species tripped traps one time each during 1615 trap nights), decreasing some of the most expensive costs associated with python trapping (labor and time spent checking traps for bycatch). They then evaluated the traps for efficacy in trapping wild Burmese pythons with the addition of a cellular-network-based game-camera system to remotely monitor traps. The game cameras were programmed to send photos to a specified email to allow daily trap checks without requiring site visits (Gati et al. 2020). Traps were placed in areas of suspected or known presence of pythons and their prey, and were baited to attract python prey, primarily small mammals, using sardines, oats, and dry dog food, and thus python-specific attractants were not used. During 2019–2020 at both L-37 and LNWR, only one non-target animal (raccoon) was captured during 3,144 trap nights. No pythons were captured, nor were pythons observed on cameras or during routine trap checks every two to three weeks (i.e., Tomahawk model 463 traps have not yet captured free-ranging pythons; Gati et al. 2020). Of the 3,144 trap nights, 99.8% (3,138 trap nights) traps were never tripped, despite all 22 traps being visited by 7–14 non-target species (primarily mammals; Gati et al. 2020).

Cost of trapping

Trap costs vary by design but a large reptile trap (i.e., Tomahawk Model 463) with a shade cover costs approximately $185. Thus far, large reptile traps used in Gati et al. (2020) have not captured free-ranging pythons and only three pythons have been

captured using box traps containing bait (Reed et al. 2011). Ultimately, the cost of traps is a very small proportion of long-term trapping costs, which are overwhelmingly comprised of labor and transportation costs.

Challenges with trapping

Operational costs can restrict large-scale trapping efforts (reviewed in Reed and Rodda 2009). Because effort and costs of trapping scales with number of traps and trap spacing, the size of an area that can be targeted with trapping can be limited by habitat accessibility and resources (e.g., funding, housing, vehicles, personnel). Some of this cost may be reduced if cellular networks exist in areas of interest and can be reliably paired with game camera systems (e.g., Gati et al. 2020). Traps must also be large enough to accommodate adult pythons, which results in significantly greater challenges to fabricate, move, deploy, and store compared to traps sized for native snake species. Along these lines, modifications to live reptile traps have been explored by replacing the rear removable door with lightweight mesh laundry bags to permit pythons of any length to be captured within the traps, but these catch bags have not been thoroughly evaluated (J. Humphrey, USDA, Written Communication, 2/4/2022). Additional considerations for traps used in southern Florida are that they likely need to be placed near water (see Habitat Use section) and to avoid flooding, should accommodate a wide variety of water depths and periods of inundation typical of the Greater Everglades Ecosystem (Lodge 2010), and these modifications further increase cost and difficulty.

Thus far, the main practical failing of traps appears to be a lack of either a suitable attractant or traps that pythons will enter (see Foraging Strategy and Trapping Experiment sections). Instead of prey bait, other attractants may prove useful for luring and capturing pythons in traps, including sex pheromones (see Pheromone section). However, pheromonal lures for use in traps have not been developed, and it is unclear how aspects of pheromone volatility and distance may influence their effectiveness. Other trap efforts may include large, portable (i.e., lightweight, collapsible) traps deployed during the breeding season, containing a wild-caught reproductive female as an attractant; trials with these traps are ongoing but thus far have not been effective (M. McCollister, NPS, Written Communication, 9/19/2022). In conjunction with different attractants, captive and field experiments with traps could incorporate drift fences along with replicated trap trials in python-occupied natural habitats with varying resource densities (e.g., mates, prey). Drift fence arrays are designed to intercept moving animals (Enge 1997) and may capture more individuals during the breeding season when movement increases (Reproduction and Movement sections), particularly if paired with a reproductive lure (e.g., sex pheromone, live reproductive female, etc.) and reinforced to dissuade pythons from climbing over the fence.

Overall, efforts thus far suggest that trapping for Burmese pythons is not currently a viable method of population control or eradication because python movement and behavior renders the snakes unlikely to regularly encounter traps. Ultimately, traps are one of a variety of control tools that managers may choose from. Future modi-

fications that result in consistent python captures might make traps a cost-effective tool for local python control, or aid in early-detection efforts in newly invaded areas (Reed et al. 2011).

Pheromones

Scent trailing using pheromones is the principal mode of reproductive communication in snakes, allowing individuals to locate each other by detecting chemical compounds from the skin (Parker and Mason 2011). Pheromonal communication signals are critical in mate searching and formation of breeding aggregations (Mason et al. 1989), and male Burmese pythons recognize and follow scent trails from females (Richard et al. 2019). Previous research with red-sided garter snakes (*Thamnophis sirtalis parietalis*) and brown treesnakes demonstrated that adult male snakes can be chemically feminized via cross-sex hormonal manipulation (Parker and Mason 2012; Parker et al. 2018). More specifically, males of both species were chemically feminized with estradiol implants, the dominant female sex steroid hormone known in these snakes, and subsequently became attractive to other males, most notably in field bioassays with wild, reproductive males (Parker and Mason 2012; Parker et al. 2018). Development of pheromonal lures for Burmese pythons has been initiated using hormonally manipulated male pythons with estradiol implants following methods of Parker and Mason (2012, 2014) in conjunction with radiotelemetry of scout snakes (see Scout Snake section) and Y-maze experiments on scent trailing (Parker and Currylow et al. 2021). Preliminary analyses revealed that telemetered, estradiol-implanted males were no different than controls in the number of associated pythons detected, indicating that estradiol manipulation failed to enhance removal efforts at the time of year and doses trialed (A. Currylow, USGS, Written Communication, 4/13/2021). Further research in reproductive physiology is needed to advance pheromonal lures as management control tools. Sex-hormone profiles, pheromone production, field chemical ecology, and reproductive behaviors are integrated and interdependent as well as seasonally variable and sex-specific, but they are not well-studied in Burmese pythons, which poses a major barrier to the development of chemoecological techniques to attract or control pythons.

Scent detection dogs

The powerful olfactory receptors of dogs have made them useful for locating several groups of invasive, cryptic, or rare species, including plants, tortoises, birds, mammals, and snakes (reviewed in Beebe et al. 2016). Scent detection dogs (i.e., detector dogs) can alert a handler to the presence of python scent in a search area where visual surveys may not be productive because pythons are well-hidden. In turn, when detector dogs search an area and do not alert, python absence may be inferred. From November 2010 to April 2011, detector dogs were tested with free-ranging Burmese pythons at 35 locations across southern Florida, resulting in the capture of 19 pythons (Romagosa et al. 2011). Detector dogs were able to search an average of 3.51 km/h, but because

of limitations from overheating, dogs could generally only work 8 km/d depending on ambient temperatures (Romagosa et al. 2011). Detector dog teams were compared to human-on-foot search teams in a series of controlled searches for known pythons in 50 × 50 m plots and along a canal. Dog teams performed similarly to human search teams in their overall success rates during plot searches for known radio-tagged pythons (73% and 64% respectively), with reduced success observed in plots with thick vegetation for both teams. The dog search team had a higher success rate in the canal searches (92%) compared to the human search team (64%). In both types of controlled searches for known pythons, dogs performed searches approximately 2.5 times faster than human searchers (Romagosa et al. 2011).

Dog characteristics important for python detection include a strong play drive, independence, and confidence because they must work for long periods of time. They must also be in very good physical condition given the temperatures, terrain, and long distances required for searching (reviewed in Troisi et al. 2019). As there may be time between detections of wild pythons, any dog used for python detection requires additional motivational trials through bagged or telemetered pythons placed along search routes (Romagosa et al. 2011). An additional challenge is the subsequent capture of the detected python in cases where the python is in an inaccessible location such as in limestone solution holes, or under water or debris (Romagosa et al. 2011, FWC 2017).

Overall, dogs can be used as a complement to other control tools. Dogs are most useful in situations where chance of human detection is low, such as assessment of python presence along areas peripheral to their current spatial range (e.g., Fig. 6; Romagosa et al. 2011). If dog behavior suggests that pythons are present in a peripheral area, then additional surveys incorporating other methods can be focused in that area to monitor occupancy and potentially contain the spread from surrounding areas (Romagosa et al. 2011).

Cost of scent detection dogs

The cost estimate for detection dogs (as with all control tools) may vary according to management area or agency and may change over time. The purchase and maintenance of a dog program from an established canine performance program over the 8-year work life span of two dogs was estimated in 2011 to be approximately $561,200 (first year: $106,200, following 7 years: $65,000 /year; Romagosa et al. 2011). These costs include a 2-employee team consisting of a handler and a snake technician, as well as food, veterinary care, and other dog maintenance supplies; this estimate does not include travel, housing, and employee benefits. Leasing two dogs, a handler, and a technician for three months, was estimated at approximately $30,240, compared to $12,000–19,000 for two techs or full-time employees, respectively. While the cost of a detection dog team is 1.5 to 2.5 times the cost of human searchers, the dog team may cover nearly 3 times the distance as a human search team on foot and may be particularly beneficial for python surveys along canals and roadways (Romagosa et al. 2011) that do not have vehicle access (i.e., preclude Road Surveys). However, since removal

programs began in 2017 (see Removals section) most visual surveys along canals and roadways are conducted by vehicle, thus covering considerably more distance than dogs and are likely more cost-effective for detecting pythons when the target areas are canals or levees (FWC 2017).

Toxicants

Several commercially available products are lethal to snakes when ingested (Brooks et al. 1998) and acetaminophen has been used, along with other methods, to control invasive brown treesnakes in Guam (Siers et al. 2019, 2020). In the case of brown treesnakes, an 80 mg dose of acetaminophen is lethal after less than 48 hours and has been deployed in the landscape via aerial and stationary bait stations containing dead neonate mice implanted with the drug (Siers et al. 2020). In Guam, where there are few native species that might also consume this toxicant (either primary or secondary consumption), this mouse-drug delivery system is effective and economical (Savarie et al. 2001; Clark et al. 2012; Siers et al. 2019). However, in southern Florida there are many native species (e.g., birds, reptiles, mammals) including state and federally listed species of concern, that would readily consume a similar type of bait system, or an animal that has previously consumed the bait, and may likewise be susceptible to acetaminophen, especially given the higher lethal dosage for Burmese pythons (i.e., 263 to 703 mg/kg; Mauldin and Savarie 2010). Therefore, although Burmese pythons may consume recently dead rodents and quail containing acetaminophen (Mauldin and Savarie 2010), the delivery mechanism and strategies to present such a bait to pythons, while excluding non-target species, is an enormous challenge. Currently, known toxicants are not a viable option for control of Burmese pythons.

Control tool summary

Existing control tools outlined thus far may work well in combination, and on a small scale within a narrow timeframe or range of circumstances (Table 4). For example, several tools are exclusively used as methods to detect python presence, including camera traps and eDNA, (see Environmental DNA section). Other more expensive methods can both detect and lead to python removals, but these are labor intensive and have resulted in few, if any, captures (e.g., scent detection dogs, mowing, telemetry of prey animals, drift fences and traps; Table 4). Visual surveys (road cruising) can be labor intensive but result in a larger number of pythons removed compared to other efforts. However, visual surveys occur primarily along roads, yet most of the invaded landscape in southern Florida is > 1 km from a road (Figs 1, 6), and these remote areas can sustain populations. Further, visual surveys result in removal of mainly young, non-reproductive individuals (see Removal and Scout snake sections). Conversely, scout snakes can lead to removal of pythons from remote areas and effectively target adult pythons with a high reproductive potential. However, this method is expensive, labor intensive, and does not remove nearly as many individuals as road cruising. While a combination of

tools may reduce python population size in a small area, the complexity and variety of habitats across southern Florida make scaling up challenging. Difficulties applying existing control tools are a result of low individual python detection probability, limited information on metrics necessary to evaluate population growth rates (i.e., abundance and vital rates), and the vast and largely inaccessible wilderness of the Greater Everglades Ecosystem (see Detection and Survival sections). Currently, available control tools are unlikely to result in eradication of introduced Burmese pythons because the population is well-established and distributed across a large and complex landscape. However, local eradication or population suppression at larger geographic scales may be feasible (Reed and Rodda 2009; Willson et al. 2011) but has not yet been attempted in a rigorous manner (e.g., focus on one area using multiple control methods).

Future research

Over the past two decades, we have learned much about the biology and management of Burmese pythons. However, most of this information comes from isolated, relatively small-scale studies at few locations, or extensive incidental (i.e., not question-driven) data derived from python removals across southern Florida. Recently, multiple federal, state, and non-profit entities have combined efforts to accomplish targeted long-term studies at broader scales. This approach will attempt to generate estimates of abundance, detection probability, and vital rates for effective decision making and management of the python population (see Demography section). Suppressing Burmese python populations throughout vast and complex wilderness habitats that are managed by many different government, state, tribal, and private entities is a daunting management challenge that can be strengthened by basic and applied research studies. Below we outline some general research strategies and themes for future work.

Population suppression

Burmese pythons are now established across a large area of southern Florida, minimally encompassing areas from Palm Beach County, south to Key Largo, and west throughout Collier County (Figs 1, 6). Eradication of the entire population across the landscape is not possible with any existing tools, whether applied singly or in combination. Similarly, eradication at smaller scales is hampered by immigration of pythons from outside the area of interest. However, suppression of localized populations may be feasible at small scales using intensive survey and removal efforts in conjunction with a suite of complementary detection and control tools along with incorporation of enhanced models for estimating population trends to assess efficacy of suppression efforts (e.g., Link et al. 2018; Davis et al. 2021; see Refinement of Existing Control Tools section). Because python detection probability is so low, by the time pythons are observed regularly, they are likely already well-established. Suppression and long-term management may also include protection of high-value resources such as bird rooker-

ies, threatened and endangered species habitat, and human-use areas (e.g., neighborhoods, agricultural areas). Suppression in these high-value areas requires careful consideration of the effect of python removals to make the best use of available research and conservation dollars (see Removal Program and Challenges, Interpreting Removal Data, and Demography and Management sections). Finally, python removal programs are in a unique position to observe declining capture efficiency, where continuing to search previously high-density areas may prevent local population recovery and document declining density (see Removal Programs section).

Refinement of existing control tools

Over the past two decades, much effort has gone into exploring control tools for Burmese pythons. Existing technologies (road surveys, visual surveys, scout snakes) that can result in python captures have advanced from initial research ideas to implementation by management agencies. Nonetheless, there are ample opportunities to refine these control tools, and some of these opportunities are described above (see Control Tools section).

Relatively little research has rigorously attempted to quantify detection via these methods (but see Nafus et al. 2020), and as a result, there is little information on individual, temporal, or spatial variation in python capture probability or how detection changes with python density, which hinders our ability to predict how management actions scale across time and space. Successful management of another invasive snake (*B. irregularis*) has largely resulted from a wide array of experimental studies that rigorously validated various control methods (see Long-term Projects and Infrastructure). Although complex control tools such as genetic biocontrol are being explored for use in python management, these tools are currently unproven and if effective will, likely take many years to develop (see Development of New Control Tools section). Current work to understand when, where, and how to apply such tools is ongoing. Likewise, evaluation of efficacy of existing control tools can be facilitated by baseline python vital-rate estimates to inform targeted management of the species (see Demography section). For example, the proportion of females that reproduce annually versus biennially is unknown, thus knowledge of fecundity is incomplete. Similarly, there are few data on survival or growth for any age class, and only recently have the first estimates of hatchling survival become available for one site with a relatively small sample size (Pittman and Bartoszek 2021). Therefore, constructing a complete Burmese python life table encompassing variation in survival and reproductive rates across age classes is a critical next step. With a complete life table, a structured population model can be developed, enabling projection of population growth rates over time. Additionally, a life table can provide an understanding of the impacts management actions have on abundance (e.g., quantify population-level effect of python removal programs) as well as direct control efforts (i.e., identification of the age/size/stage class that most influences population growth rates). As such, development of a structured population model is an important step in maximizing effectiveness of existing control tools (e.g., road

and visual surveys, scout pythons) and informing development of new tools. Studies that provide data on vital rates and ultimately inform abundance estimation are conducted via capture-mark-recapture surveys (see Demography and Density sections), and while difficult to obtain (see Detection section), the use of radiotelemetry to locate snakes can help provide these data (see Survival section). Ultimately, implementation of nearly any major control effort will be difficult without the ability to monitor resulting shifts in abundance and thus rigorously assess efficacy (see Abundance section).

Baseline abundance estimation

Overall, despite removal of many Burmese pythons over the past several decades (Fig. 7) throughout the landscape, we know little about population size or trends over time for any area. However, without abundance information or minimally a reliable index of abundance, evaluating the effectiveness of current or proposed control methods with respect to effort and cost remains challenging. Going forward, further development of novel methods may be promising for estimating python abundance. For example, removal of unmarked animals (without release), is common for management and monitoring of invasive species (e.g., invasive carp, Cupp et al. 2021), yet it does not account for variation in detection, rendering interpretation of removal counts challenging (Anderson 2001). Removal models have been developed to estimate abundance based on removals of animals from a population (Moran 1951; Zippen 1956) and have been expanded to incorporate spatially distinct sites that are demographically closed (Dorazio et al. 2005, 2008; Ruiz and Laplanche 2010; Davis et al. 2016), sites with open populations (Matechou et al. 2016), and robust design (Link et al. 2018; Udell et al. 2022). Recently, removal models have been extended to better match the management time frames of invasive species control (i.e., years). For example, invasive lizard removal data has been integrated into a robust design framework that estimates abundance and demographic processes (Link et al. 2018). Building on that work, Davis et al. (2021) developed a framework to estimate invasive species abundance, evaluate management effectiveness, and population growth rate over time from various removal techniques of invasive feral swine. As such, removal models may represent an avenue by which ongoing python removal data may be incorporated into research to generate abundance estimates for specific locations. However, although some removal models account for imperfect detection, challenges with low individual detection probability in pythons, particularly in areas that are difficult to survey (i.e., away from roads) likely still present significant challenges for implementing such models.

For removal models to be informative they must (1) account for effort, (2) be targeted to a defined area, ideally with effort equally spread across the area to minimize heterogeneity in detection, and (3) have enough removal pressure to result in a substantial reduction in abundance. For example, Link et al. (2018) developed and applied a removal model to an invasive population of veiled chameleons (*Chamaeleo calyptratus*) that had been subject to long-term eradication efforts. The removal model used data from 11 sites selected over a region encompassing the original site of the introduction

(9 primary sampling periods, each with removals conducted on up to 3 occasions) for a total of 203 surveys over one year (2004–2005; Link et al. 2018). Results suggested there were initially 30 chameleons (95% credible interval 19 to 55) in the population and removal efforts in the third year of effort estimated approximately 3 chameleons remained (95% credible interval 0 to 11; 87.2% chance that lizards remained). Indeed, the following year (2005–2006), 5 more chameleons were captured in 147 attempts, and by 159 subsequent attempts over the next 5 years none were captured, suggesting that the eradication program was successful. Importantly, this study required a large degree of effort (Link et al. 2018) for a species that can have relatively high detection probability in nocturnal visual searches (e.g., Jenkins et al. 1999; Shirk et al. 2014), and the approach may not translate well to pythons. However, this example illustrates (1) the need for consistent data collection across all entities and (2) the multi-year requirement necessary to achieve all three components (i.e., account for effort in a defined search area with consistent removal pressure). Thus far, no coordinated effort that meets these criteria has been attempted for pythons. Future work to ensure all three components occur simultaneously could be valuable, both for removal programs aiming to suppress pythons in localized areas of southern Florida, and to evaluate the utility of removal models.

Removal approaches may also provide additional information to evaluate management actions by incorporating close-kin mark-recapture to infer population demographics. Close-kin mark-recapture identifies close-kin pairs (e.g., parent-offspring, half siblings) using genetic sampling of individuals and has been applied to assess relatedness of fish species in both fresh and saltwater systems to infer population sizes (Bravington et al. 2016; Hillary et al. 2018; Ruzzante et al. 2019; Wacker et al. 2021). For example, using the genetic relatedness of live and dead juvenile white sharks in a close-kin mark recapture framework, direct abundance estimates of 280–650 adults have been estimated for sharks in New Zealand and Australia. These estimates are more precise than previous methods (e.g., generational effective population size or number of breeders) because only the juvenile white shark age class can be easily sampled (Hillary et al. 2018). Unlike classic mark-recapture which requires repeated encounters of individuals, close-kin mark-recapture estimation uses a genetic match to identify parents, and this approach could be applied to removed pythons that have only a single encounter. Thus far, robust removal extensions and close-kin mark-recapture are in the early stages of evaluation for Burmese pythons.

Relative abundance and abundance indices

Once population abundance has been estimated for a given location, a baseline exists to monitor resulting shifts in abundance. After developing a baseline, simpler and less-expensive methods such as an index of abundance could be evaluated (and calibrated) to track changes in abundance over time and space (Engeman 2005; Janousek et al. 2019; Bauder et al. 2021). Multiple indices can be simultaneously evaluated, and concordance among estimated trends (i.e., similarity in trend direction, duration, and

magnitude) may indicate that sampling methods are effective in mirroring trends in true abundance (e.g., Bauder et al. 2021). Additionally, development and validation of novel methods that do not rely on capture-mark-recapture may be promising for estimating python abundance. For example, a study of killer whales in British Columbia compared line transect and mark-recapture estimates from small-boat surveys to true population size, known from censuses (Williams and Thomas 2009). Both methods produced estimates close to the true population size, and despite small sample sizes and violations of some model assumptions, may be considered useful to assist status assessments with appropriate caveats (Williams and Thomas 2009). Other considerations are that index methods often rely on the assumption that the index is linearly related to absolute abundance, and that this relationship is constant over space or time, which may be incorrect.

Expanding current removal efforts (e.g., see Removal Programs section) may provide an avenue to track changes in relative abundance over time. For example, a useful initial index to compare with more rigorous abundance estimates could include systematic road surveys (without removal) at regular locations over time, while recording number of pythons along with search effort and variables expected to influence python detection (e.g., weather, survey hour, observers, season). Developing initial abundance indices using road surveys in focal areas or research sites would require coordination among agencies conducting removal efforts to ensure standardized surveys where pythons were recorded but not removed. Improving current removal protocols to include surveys within a larger grid area overlapping road transects, where researchers would survey throughout the area using a mark-recapture framework with radiotagged pythons (see Abundance section), may provide information for abundance as well as survival estimation (e.g., known fate analysis; Newcomb et al. 2016). In addition to radiotags, pythons in the larger grid area could be visibly marked to be incorporated into the abundance index component. Pythons that are visibly marked (e.g., brightly colored T-bar style Floy tags, see Scout Snake section) and crossing roads may provide rough estimates of individual detection in areas being targeted by people removing pythons.

Long-term projects and infrastructure

To be effective, efficient, collaborative, and ultimately successful in population suppression, future Burmese python research would require multi-year studies at the landscape scale, coordinated across multiple organizations with consistent effort-both in terms of funding and labor. One example is multi-year funding for collecting data to estimate key python demographic parameters (e.g., reproductive frequency, age-specific fecundity/survivorship) that are required to develop, evaluate, and ultimately maximize efficacy of control tools. Additionally, development of a facility in southern Florida for captive and small-scale manipulative trials could be useful to refine and optimize the application of control tools and explore techniques better equipped to handle low detection. Unlike the 5-ha enclosure built to enumerate a wild popula-

tion of brown treesnakes and evaluate detection probability under various control approaches (e.g., Tyrrell et al. 2009; Christy et al. 2010; Amburgey et al. 2021), a similar enclosure in southern Florida could not feasibly enclose an experimental population because pythons are much larger and more mobile than brown treesnakes (35–160 cm SVL, Tyrrell et al. 2009; Christy et al. 2010). Instead, a facility in southern Florida with large, enclosed areas (e.g., 75 m^2) could facilitate targeted experiments in a more natural environment, with a similar climate to the native range, for studies of behavior and physiology (e.g., attractants, see Trapping section). Further, a facility for future genetic or other biocontrol tool assessment may be important although it would require high levels of biosecurity to contain pythons during reproductive research (see Development of New Control Tools section).

Biologging tools to inform python behavior

Monitoring individual animals *in situ* has the potential to reveal important aspects of a species' ecology such as seasonal and daily activity patterns, foraging strategies, or reproductive behaviors, and this approach may reveal vulnerabilities for control tool development or may improve python detection. The rise of electronic biologging devices in the last two decades has unlocked a wealth of information about animal space use, movements, and physiology (e.g., Cagnacci et al. 2010; Williams et al. 2020). For example, tracking the locations of Burmese python breeding aggregations has revealed that breeding in ENP is likely to occur in lowland forests (often tree islands, Smith et al. 2016).

Technological advances in tags deployed in or on wildlife (i.e., biologging tags; Whitney et al. 2021), such as increased battery life and memory capacity as well as sensor design, may also help to accelerate the speed, quality, and volume of information on python ecology and behavioral patterns. For example, miniaturization of batteries has allowed smaller sensors to be placed within tags, enabling not only tagging of smaller individuals, but also detection of acceleration and fine-scale movement patterns of individuals in the wild. In addition, innovative technology such as two-way tag communication (i.e., proximity tags, Ripperger et al. 2020) that record interactions between predators and their prey, could be used to improve future studies designed to decipher impacts of pythons. This technology could enable a more detailed understanding of python activity patterns that could be exploited to increase removal success.

Although GPS-tracking of pythons has typically had low success (Smith et al. 2018), focused partnerships between researchers and tag manufacturers may produce satellite tags that can be implanted in pythons to relay locations that transmit at regular intervals via a system of satellites, rather than storing data on tags directly (Klimley 2013). Recently launched lower-orbiting satellites (cube sats; Poghosyan and Golkar 2017) may one day allow more precise logging of python positions, which could improve the number and location accuracy of positional data in ongoing scout tracking projects. In addition, acoustic telemetry in aquatic environments along southern Florida's network of canals may inform python use of canals and marsh habitats at

times when researchers are not present, because tags transmit at regular intervals and each tagged animal can be detected on receivers deployed throughout the landscape. Further, combining multiple sensors in a single animal tag can yield complementary information. For example, accelerometers can be paired with GPS tags to combine data collection on fine-scale behavior with large-scale movements (Whitney et al. 2021). Advanced behavioral modeling algorithms are also emerging (e.g., Jeantet et al. 2020; Cullen et al. 2022), which could reduce the need to simultaneously observe individual behaviors in animals equipped with biologging devices. However, novel statistical analyses are needed to extract patterns from data streams coming from multiple sensors with differing temporal resolutions (McClintock et al. 2017) before simultaneous observations are not needed. Other tools not yet employed could include remote monitoring using drones with specialized telemetry payloads or two-way communication options with python radiotags that can relay locations to listening stations such as stationary structures or mobile animals (e.g., Kline et al. 2021).

Development of new control tools

With the rapid evolution of technology, new control tools could be applied to aid Burmese python management. Although research may continue to lead to better understanding, optimization, and implementation of existing control technologies to fully evaluate their impacts and transferability in new locations, investments in novel technologies have the potential to yield high rewards. One example is the rapidly growing field of genetic biocontrol, where genetic material is manipulated with the goal of decreasing the ability of an invasive species to thrive in the non-native environment. Genetic biocontrol methods have primarily been used to control disease-carrying pests in laboratory experiments (e.g., mosquitos, Hammond et al. 2021) and are designed to be species-specific to avoid impacts on non-target animals and plants (Harvey-Samuel et al. 2017). Replicating genetic biocontrol technologies effect changes in the genome which allow for heritable material to be passed down to subsequent generations and could, for example, result in generational shifts in sex ratios or promote infertility that could help induce population collapse. A primary benefit to genetic biocontrol is that the tool does not rely exclusively on human detection, which has been the primary means of removing large numbers of Burmese pythons from the landscape. Furthermore, genetic biocontrol approaches that rely on reduction of natural reproductive success could be considered more humane than control technologies that rely on chemical poison, trapping, or shooting (Faber et al. 2021; see Toxicant section).

An example of a potential gene drive target in Burmese pythons includes targeting and destroying the X chromosome (Gamble et al. 2017) during spermatogenesis, leading to male-biased (OY gametes) sex-ratio distortion that could promote population collapse. This strategy was developed by Galizi et al. (2016) for the biocontrol of the malaria vector (mosquito) *Anopheles gambiae* and could be applicable to other organisms that rely on genetic sex determination. This method would require the release of

a percentage of genetically modified individuals to allow for transfer throughout the population of the mutation through breeding.

Alternatively, non-replicating species-specific RNA interference (RNAi) technologies disrupt physiological functions in a target organism to reduce reproductive output or cause death through ingestion or topical application to a target organism (e.g., Xu et al. 2021). A critical component and benefit of the technology is that the RNAi compound can be developed and validated to be species-specific, ensuring other species are not harmed (e.g., only functional in Burmese pythons). RNAi control applications in Burmese pythons would likely require recurrent deployment across a vast area and uptake of the compound by the targeted organism, in some cases through ingested baits. Scientific evaluation of practical considerations such as these would be required before implementation. RNAi compounds might be a useful tool for small, high-value ecological areas, or in combination with chemical attractants for baiting into an area.

Although Burmese pythons are thought to primarily be ambush predators, they do engage in active foraging (see Feeding Strategy section), and if effective prey-scent attractants are developed, they may lure pythons into the area to feed on an RNAi bait and possibly into a trap. Development of control tools that concentrate individual pythons in time and space such as continued refinement of chemical attractants (see Pheromone section) or development of food-based attractants may be valuable tools for population suppression efforts. As with any novel biocontrol technology, this line of research is a longer-term investment strategy but has the potential to increase removal efficiency.

Technical aspects of the research

While potentially powerful, genetic biocontrol technologies are relatively novel in vertebrates (Horak 2020; Teem et al. 2020). As with the majority of control techniques, these tools are potentially expensive and complicated, requiring laboratory work (e.g., investigation of genetic sequences) permitting, regulation, public engagement and approval, and specific information on python life-history parameters (see Demography section). However, some avenues such as *in vitro* work utilizing living cell lines are being explored as a valuable avenue to further explore genetic biocontrol methods with fewer logistical and regulatory constraints. Despite a sequenced genome for Burmese pythons, characterization of genes and pathways are severely limited (Castoe et al. 2011) and development of genetically modified reptiles is in the early stages, such as the microinjection of CRISPR-Cas9 components into immature oocytes to produce targeted mutations in anoles (Rasys et al. 2019). Furthermore, the development of gene drive strategies for sex ratio distortion is complicated by the limited information on the location of genetic sex determination elements (Gamble et al. 2017). Devising appropriate strategies and assessing putative targets in a reptilian system lacking a genetic toolbox will require testing basic mutagenic approaches *de novo* (e.g., transfection). *In vitro* mutagenic and transgenic work in *P. bivittatus* has recently begun and may help lay the foundation for similar work in other reptiles of interest (e.g., *Boiga irregularis*).

Table 5. Glossary.

Term	Definition
Active thermoregulation	Behaviors used by ectotherms such as basking, seeking shade, or altering body posture to change heating and cooling rates
Ambush predator	Sit-and-wait predators that capture or trap prey by stealth or luring behaviors
Biennial reproduction	Breeding every two years
Brumate	Metabolic adaptation in reptiles allowing them to conserve energy by becoming dormant during cold temperatures
Capture mark recapture	CMR; Capturing many organisms, marking them, releasing them back into the population, and then determining the probability of capture (i.e., ratio of marked to unmarked animals in the population)
CRISPR-Cas9	Programmable protein ribonucleic acid complex used to target and edit specific DNA sequences
Critical thermal minimum	Low temperature at which mobility is lost; if temperatures continue to fall the lethal thermal minimum is reached, leading to death
Cryptic species	Visual, olfactory, or auditory concealment by an organism to avoid detection as a predation or antipredator strategy
Dietary generalist	Organism that consumes a wide variety of foods
Dispersal	Unidirectional movement of organisms away from place of birth
Early Detection & Distribution Mapping System	EDDMapS; Geospatial database of invasive species reports. https://www.eddmaps.org/
Ectotherm	Organisms that rely on environmental heat sources to control body temperature
Energy budget	Quantification of the uptake of energy from the environment by an organism (feeding and digestion) how that energy is spent including for maintenance, development, growth, and reproduction
environmental DNA	eDNA; DNA released from an organism into the environment
Everglades virus	An alphavirus included in the Venezuelan equine encephalitis virus complex
Home range	Area used by an animal during normal activities such as foraging and mating, but excluding occasional exploratory excursions
Labyrinth morph/phenotype	Maze-like dorsal pattern selectively bred into the commercial snake/python trade
Lacey Act	United States law created in 1900 to restrict illegal wildlife trade, bar international importation of injurious species, and protect species at risk
Movement ecology	Subdiscipline of ecology connecting connects an animal's movement path with environmental heterogeneity, available resources, navigational capacity, and its biology
Multiple paternity	More than one male siring a clutch or litter
Nidovirus	Diverse order of enveloped positive-strand RNA viruses that infect a range of vertebrate and invertebrate hosts and can cause serious diseases
Non-replicating, species-specific RNA interference	RNAi; Process where species-specific RNA molecules affect gene expression of key processes that impact an organism's fitness
Occupancy model	Approach to estimate probability that a species will occupy a site
Osmoregulation	Active regulation of an organism's body fluids to maintain electrolyte concentrations (i.e., prevent fluids from becoming too dilute or concentrated)
Oviposit	Lay eggs
Parthenogenesis	Spontaneous development of an embryo from an unfertilized egg cell; reproducing without a male or stored sperm
Pentastomes	Parasitic arthropods requiring one or more intermediate hosts before completing its life cycle in a definitive host
Polymerase chain reaction	PCR; laboratory technique for rapidly producing (amplifying) millions to billions of copies of a specific segment of DNA for genetic analyses
Radiotelemetry	Attaching or implanting a transmitter to an animal and using a receiver and directional antenna to locate it over space and time
Scout snake	A radiotagged snake used to locate untagged snakes
Shivering thermogenesis	Generation of heat by repeated contraction of muscles
Serpentovirus	Also known as reptile nidovirus. See also: nidovirus. Virus that causes severe and often fatal respiratory disease, typically in captive snake species, especially pythons
Snake fungal disease	SFD; Infectious disease found in many snake species caused by the fungus *Ophidiomyces ophidiicola*
Spatial capture-recapture	SCR; Extension of capture-mark-recapture used to estimate population density from detections and subsequent redetections of individuals across space
Species or Individual detection	Chance that a species or individual will be detected during a survey, given that it is present at the location
Snout-vent length	SVL; Measurement of size taken from tip of nose to opening of cloaca, at base of tail
Survey	Ecological census conducted via a variety of methods to collect data on occupancy of habitats by an organism
Total length	TL; Measurement of size taken from tip of nose to tip of tail

Gene drive regulation and stakeholder engagement

Regulation on gene drive systems is a rapidly evolving topic governed at international, regional, and national levels (NAS 2016; Redford et al. 2019). The regulation of engineered gene drives is currently under development to allow for appropriate incorporation into existing frameworks addressing pest control, animal drugs, toxins, or environmental protection (Oye et al. 2014). Despite the potential of genetic biocontrol to mitigate the highly harmful impact of invasive species, approaches such as gene drives can be controversial as they have the potential to affect non-target populations that share a close genetic relationship to the targeted invasive species (Teem et al. 2020). Moreover, without appropriate safeguards to address unimpeded propagation of the genetic biocontrol mechanism, these technologies could also impact the targeted organism in its native range. Therefore, stakeholder engagement via informal interviews, closed workshops/focus groups, direct meetings, or local/regional surveys (e.g., Shackleton et al. 2019) have been applied to help navigate concerns with implementation of these technologies for control of Burmese pythons.

Demography and genetic biocontrol

Developing and evaluating genetic biocontrol methods will require information on python life history parameters such as the prevalence of multiple paternity, sex or age specific survival rates, and variation in fecundity (see Demography section). Overall, there is little information on the size, population growth, or demographic structure of current python subpopulations. These data gaps may impede efforts to evaluate any applied genetic biocontrol tools and likewise prevent comprehensive understanding of how many biologically manipulated individuals would need to be released on the landscape to yield population declines. Recent and active progress is being made by USGS and others to fill these data gaps on life history knowledge (e.g., Soto-Shoender et al. 2020; Bartoszek et al. 2021b; Josimovich et al. 2021; Pittman and Bartoszek 2021; Taillie et al. 2021; Vishnu et al. 2021; Whitney et al. 2021; Anderson et al. 2022; Currylow et al. 2022b).

Conclusions

Burmese pythons in southern Florida represent one of the most intractable invasive-species management issues across the globe. The problem stems from a unique combination of inaccessible habitat with the cryptic and resilient nature of pythons that do very well in the subtropical environment of southern Florida, rendering them extremely difficult to detect. We have documented extensive direct alteration of the native food web as well as some aspects of the basic biology of these giant constrictors over the past two decades, while extensively exploring methods to capture and remove this damaging species (Table 4). However, very low individual detection probabilities for Burmese pythons remain the greatest obstacle to developing landscape-scale control programs. Controlling population expansion and minimizing the impact of

pythons to natural resources is a pressing concern as billions of dollars have been spent in attempts to restore the Everglades after more than 100 years of extensive wetland alteration (Davis and Ogden 1994; Clarke and Dalrymple 2003; Finkl and Makowski 2017). Consequently, invasive species, including Burmese pythons, represent one of the greatest threats to restoration success (e.g., Center et al. 2012). Biological invasions have cumulatively caused at least $1.22 trillion in economic losses in the United States over the past six decades, with the largest impacts coming from mammalian, plant, and insect invaders (Fantle-Lepczyk et al. 2022). For example, in the southeastern United States, costs to control feral pigs and citrus canker have totaled $460 and $420 million, respectively (Fantle-Lepczyk et al. 2022). Excluding research expenditures, considerably less has been spent to manage Burmese pythons, with approximately $10.6 million since 2004 (USFWS 2012).

Although a wide variety of techniques have been employed to catch pythons across southern Florida, many of these tools have not been evaluated rigorously, largely because of difficulty detecting pythons. Although rapid response to reports of individual pythons in new areas is ongoing, there have not been any concerted efforts aimed at suppression or eradication of python populations, even in limited areas. Cost-effective control methods and a better understanding of impacts on natural resources may help to inform application of limited resources and development of mitigation strategies. Because of individual heterogeneity in snake detection (e.g., Tyrrell et al. 2009; Christy et al. 2010; Yackel Adams et al. 2019), integration of multiple control tools (Závorka et al. 2018), including existing tools as well as new methods, will likely be necessary to suppress the python population and quantify the level of suppression. Over the longer term, genetic biocontrol tools may provide an avenue towards eradication, but these tools are currently in the early stages of development for pythons. Therefore, future research to better understand and optimize implementation of existing technologies and transferability in new locations (e.g., where/when certain control methods work best, cost/benefit analysis) can help to fully evaluate python impacts. As such, important avenues of research include research into basic reproductive life history and estimation of key vital rates such as survival to project population growth rates over time to understand the impacts of management actions on abundance. Overall, eradication of pythons in southern Florida is likely impossible. Suppression of the python population, even at local scales, will require strategic coordination of researchers, land managers, funding, public outreach, implementation of several different complementary tools, and rigorous evaluation of these tools.

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Supplementary material 1

FWC SFWMD mass length

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Data type: table (excel file)

Explanation note: Burmese python (*Python molurus bivittatus*) length (SVL, cm), mass (kg), and sex recorded from 2017–2022 (n = 4,825) by contractors capturing individuals as part of Removal Programs operated by the Florida Fish and Wildlife Conservation Commission (FWC) and South Florida Water Management District (SFWMD; see Removals section). Data owned and managed by FWC and SFWMD.

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Link: https://doi.org/10.3897/neobiota.80.90439.suppl1

Supplementary material 2

Python removals WIMS data used in synthesis

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Data type: table (excel file)

Explanation note: Reported removals of Burmese pythons (*Python molurus bivittatus*) across southern Florida through December 31st, 2021 (n=13,746) used to construct Fig. 7. These data have been reported to and are managed by Florida Fish and Wildlife Conservation Commission (FWC). Pythons are predominantly removed from areas within a kilometer of a road (Fig. 6) through several avenues including the Florida Python Challenge, EDDMapS, State and Federal Agencies, and the FWC and South Florida Water Management District (SFWMD) paid Contractor Programs, initiated in 2017 (see Removals section).

Link: https://doi.org/10.3897/neobiota.80.90439.suppl2